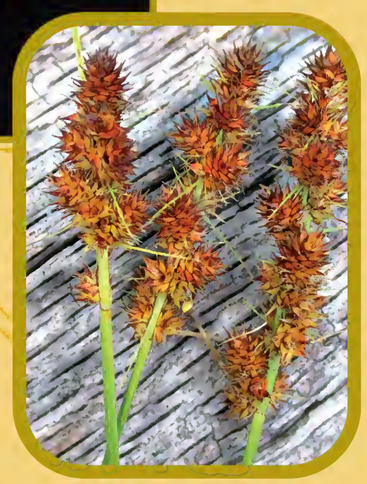
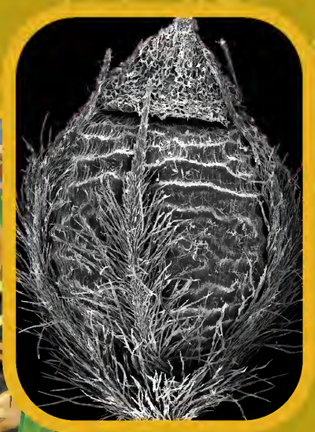
Sedges:
Uses, Diversity, and Systematics of the Cyperaceae





Robert F. C. Naczi and Bruce A. Ford, Editors

The sedge family (Cyperaceae) is one of the 10 largest families of flowering plants, with over 5000 species and 108 genera. Sedges grow on every continent except Antarctica. They occur in habitats ranging from marshes to deserts, and they dominate many ecosystems, including tundra and savanna. Some species are habitat-specific, narrowly distributed, and of conservation concern, whereas others are ubiquitous weeds that occur in a variety of environments. Many species fill key ecological roles, and others are economically important. Yet, sedges remain poorly known. Their reduced flowers and complicated patterns of morphologic variation make the identification of these fascinating plants challenging. As a result, many have avoided the study of sedges as too difficult.

Over the past decade, a marked upsurge of interest in sedges has occurred. Professional botanists, conservationists, and students have made rapid strides in understanding the ecology, economics, taxonomy, and phylogeny of the Cyperaceae. As the proceedings of the first international conference devoted to sedges, *Sedges: Uses, Diversity, and Systematics of the Cyperaceae* is a keystone of sedge literature. This volume contains 14 chapters authored by internationally renowned experts in sedge biology. Many facets of sedges are covered, both as reviews of current knowledge and as reports of original research. Topics include ethnobotany, weeds, biogeography, floristics, conservation, ecology, genetic diversity, phylogeny, and taxonomy. Both taxonomic and geographic coverage are broad: *Carex* to *Uncinia*, and boreal North America to Amazonia. Field exploration, analysis of morphologic data, molecular systematics, and allozyme analysis are among the diversity of techniques featured in this book.

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Robert F. C. Naczi
and Bruce A. Ford,
Editors

Missouri Botanical Garden
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Table of Contents

Contributors vii

Introduction ix

Acknowledgments xi

Frosted Curls to Tiger Nuts: Ethnobotany of Cyperaceae
David A. Simpson 1

The Significance of Cyperaceae as Weeds
Charles T. Bryson and Richard Carter 15

Diversity, Endemism, and Phytogeography of North American Coastal Plain Sedges
Bruce A. Sorrie 103

***Carex* (Cyperaceae) of the Kisatchie National Forest, Louisiana, U.S.A.**
Philip E. Hyatt 119

Description of the Population, Canopy Cover, and Associated Vegetation of the Globally Rare Sedge *Carex polymorpha* (Cyperaceae) in Nescopeck State Park, Pennsylvania
Jamie L. Horvath, Timothy A. Block, and Ann Fowler Rhoads 133

Segregation of Sedge Species (Cyperaceae) Along Environmental Gradients in Fens of the Schefferville Region, Northern Quebec
Anna Dabros and Marcia J. Waterway 145

The *Carex* Flora of Quebec–Labrador North of 54°N
Jacques Cayouette 163

Allozyme Variation in the Genus *Carex*...15 Years Later: 1986–2001
Leo P. Bruederle, Stephen L. Yarbrough, and Shannon D. Fehlberg 187

Phylogeny and Patterns of Convergence in *Carex* Sect. *Ovales* (Cyperaceae): Evidence from ITS and 5.8S Sequences
Andrew L. Hipp 197

East vs. West: Monophyletic Clades Within the Paraphyletic *Carex acuta* Complex, Section *Phacocystis* (Cyperaceae)
Julie A. Dragon and David S. Barrington 215

Carex Sect. _Phyllostachyae:_ The Value of a Multidisciplinary Approach in Conducting Systematics Studies in Sedges
Bruce A. Ford, Robert F. C. Naczi, and Julian R. Starr.....227

Phylogeny of the Unispicate Taxa in Cyperaceae Tribe Cariceae II: The Limits of _Uncinia_
Julian R. Starr, Stephen A. Harris, and David A. Simpson.....243

Towards a Revision of the Genus _Pleurostachys_ (Cyperaceae): Preliminary Results
William Wayt Thomas and Marccus Alves.....269

Cladistic Analysis in _Rhynchospora_ Sect. _Pluriflorae_ (Cyperaceae)
Ana Claudia Araújo, William Wayt Thomas, and Hilda M. Longhi-Wagner.....279

Taxonomic Index.....289

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Introduction

The sedge family (Cyperaceae) is one of the 10 largest families of flowering plants, with over 5000 species and 100 genera. Sedges inhabit every continent except Antarctica and occupy nearly the full range of latitudes and altitudes available to vascular plants. They occur in habitats ranging from marshes to deserts. Sedges dominate certain ecosystems, such as tundra and some savannas. Some species are habitat-specific, narrowly distributed, and of conservation concern, whereas others are ubiquitous weeds that occur in a variety of environments. In many ecosystems, they play a critical role in preventing erosion and flooding, and they furnish food and nesting sites for wildlife.

Life history diversity of sedges is high, with annual, perennial, wind-pollinated, insect-pollinated, and fire-resistant species all represented. Morphologically, sedges span habits ranging from submersed aquatics and diminutive herbs to high-climbing vines and scrubby trees. Variation in inflorescence and fruit morphology is extraordinarily diverse and provides the basis for most classifications of sedges.

Despite the great size, cosmopolitan distribution, ecologic importance, and morphologic diversity of the Cyperaceae, the study of sedges has been neglected. Historically, views prevailed that sedges were of little economic importance, difficult to identify, and morphologically intractable. Thus, many potential students of the family avoided these plants. Consequently, many sedge species remain undescribed, and relationships among most genera and species are only beginning to be understood. Over the past two decades, a marked upsurge of interest in sedges has occurred. Professional botanists, conservationists, and students have made rapid strides in understanding the ecology, economics, taxonomy, and phylogeny of the Cyperaceae.

A major point of progress in the understanding of sedges was the first international conference devoted to the Cyperaceae. "Sedges 2002: International Conference on Uses, Diversity, and Systematics of Cyperaceae" was held 6–8 June 2002 on the campus of Delaware State University, Dover, Delaware, U.S.A. The conference attracted 90 participants from four continents. Attendees represented a breadth of experiences and included students, professors, conservationists, amateur naturalists, gardeners, and environmental consultants. On the first day of the conference, 18 experts delivered presentations on subjects ranging from ethnobotany to conservation. These presentations spanned a wide range of methodologies and the three conference themes of uses, diversity, and systematics. On the second day, trips led by field botanists introduced participants to sedge diversity of the Delaware and Maryland Coastal Plain and Piedmont. The final day of the conference was devoted to several workshops on identifying *Carex* sections and species. Eight experts in *Carex* taxonomy and identification led these sessions, some of which catered to those with little prior experience, and others instructed seasoned veterans. Sedges 2002 concluded with an informal discussion about current research projects, needs, and future objectives.

The impact of Sedges 2002 is far-reaching. The conference provided an opportunity for like-minded individuals to share ideas, forge new collaborations, and renew old ones. The many student attendees had the chance to meet experts, learn from them, and receive direction in building their careers. Communication of knowledge about sedges to a large audience was another major impact of the conference. In order to augment dissemination of information about sedges and provide a permanent record of the work conveyed at the conference, we present the proceedings of Sedges 2002 in this volume.

Uses of sedges are the foci of the first two chapters of this book. The authors of these papers challenge the traditional view that Cyperaceae have little economic importance. In his review of the ethnobotany of sedges around the world, David Simpson presents evidence of widespread use of sedges by humans. These uses are as diverse as food, building materials, and papermaking. The large genera *Carex* and *Cyperus* are used most often, especially in the tropics. Charles Bryson and Richard Carter present a comprehensive review of the world's weedy sedges. They discuss many aspects of sedge weed biology and provide a list of species that are undesirable. They show that a minority of sedge species is weedy. However, these plants have a great impact on human affairs, especially agriculture.

Diversity, phytogeography, and ecology of sedges figure prominently in the next five chapters.

Bruce Sorrie examines large-scale patterns of diversity and geographic distribution for sedges occurring on the Coastal Plain of North America. He reveals that the Coastal Plain hosts nearly 500 species of native sedges, although this region represents less than 10% of the North American landmass. He also highlights the significance of the Coastal Plain as a center of sedge endemism. The North American Coastal Plain also figures prominently in Philip Hyatt's case study of sedge diversity and distribution. He investigated *Carex* species in the Kisatchie National Forest, Louisiana, U.S.A. He documents 59 taxa in the Forest, occurring in a variety of plant communities. Jamie Horvath, Timothy Block, and Ann Fowler Rhoads examine the ecology of the globally rare *Carex polymorpha* at one of its largest populations in Pennsylvania, U.S.A. Their study reveals patterns in shoot density and flowering as they relate to canopy closure and associated flowering plant species. These findings help characterize the biology and habitat of this rare sedge, and have important implications for management and conservation. Anna Dabros and Marcia Waterway studied the ecology of sedges in fens in northern Quebec, Canada. They analyze the micro-scale distribution patterns of 27 sedge species along hydrologic, chemical, and physical gradients in the environment. Their results reveal patterns of habitat specificity, which provide insights in niche partitioning among co-occurring species. Northeastern Canada is also the geographic focus of Jacques Cayouette's chapter. He investigates the floristics of *Carex* in northern Quebec and Labrador. He documents 97 taxa for the region, characterizes their habitat preferences, and reviews current taxonomic problems.

The remaining seven chapters of this volume are devoted to the systematics of particular sedge genera. Leo Bruederle, Stephen Yarbrough, and Shannon Fehlberg review the use of allozymes in studying the systematics of *Carex*. Their work underscores the utility of allozymes for revealing patterns of genetic diversity in sedges. Allozyme-based studies have proven critical for understanding sedge evolution, especially the relationship between growth form and breeding system, and the effects of dioecy on population genetics. Andrew Hipp presents a phylogeny for *Carex* section *Ovales*, one of the largest sections of *Carex* (ca. 85 species), based on DNA sequence data. His work supports monophyly for the section, resolves placement of species whose putative membership in the section had been controversial, and reveals important details of morphologic character evolution. Another large section of *Carex*, section *Phacocystis*, is the subject of the chapter by Julie Dragon and David Barrington. They reconstruct the phylogeny of the *Carex acuta* complex using DNA sequence data. In turn, they use the phylogeny to identify clades within the complex, investigate infraspecific variation in some of its members, and elucidate its biogeography. Bruce Ford, Robert Naczi, and Julian Starr review the systematics of *Carex* section *Phyllostachyae*, a subject of much recent research. They use the section as a case study to highlight the value of using diverse methodologies for resolving taxonomic problems and elucidating relationships among sedges. Julian Starr, Stephen Harris, and David Simpson consider relationships among unispicate members of the Cariceae, especially *Uncinia*, using DNA sequence data. Their work has important consequences for generic classification in Cariceae and for the use of traditional characters in the classification of *Uncinia*. William Wayt Thomas and Marccus Alves review the taxonomy of *Pleurostachys* and present new data for a revision of the genus. They reconstruct the phylogeny of the genus, based on morphologic characters. Also, they discuss the biogeography of *Pleurostachys*, finding that all 23 species of the genus are Neotropical, with most occurring in Brazil's Atlantic coastal forest. Neotropical sedges again are the focus of the chapter by Ana Claudia Araújo, William Wayt Thomas, and Hilda Longhi-Wagner. They present the results of a phylogenetic analysis of *Rhynchospora* section *Pluriflorae*, based on morphologic data. These results indicate that the traditional circumscription of the section does not reflect their new understanding of relationships among these sedges.

Sedges: Uses, Diversity, and Systematics of the Cyperaceae presents a broad spectrum of research topics, results, and concepts. We hope this book will provide an important contribution to our understanding of sedges, as well as a starting point for future studies of one of the world's great plant families.

Robert F. C. Naczi
Bruce A. Ford

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We are grateful to the many individuals who contributed their talents, energy, and time to make "Sedges 2002" a successful conference. Kenneth Bell, then Dean of the College of Agriculture and Related Sciences, Delaware State University; Richard Barczewski, Chairman of the Department of Agriculture and Natural Resources, Delaware State University; and David Punter, then Head of the Department of Botany, University of Manitoba, supported and encouraged us to host the conference. Anton Reznicek met with us on the campus of Delaware State University in August 2001 to assist with the initial planning. Keith Clancy and Christopher Frye spent many hours helping process registrations, preparing name badges for registrants, and handling other essential details in preparation for the conference opening. Louis Calabrese, Arthur Tucker, and Susan Yost assisted with procuring lunches and refreshments, securing parking, greeting attendees, and exhibiting posters. Donna Noel and Louise Stith welcomed and registered attendees.

On the first day of the conference, Charles Bryson, Leo Bruederle, Jacques Cayouette, Rick Darke, Bruce Ford, Paul Goetghebeur, Andrew Hipp, John Larson, Mary Leck, William McAvoy, Muthama Muasya, Anton Reznicek, Alfred Schuyler, David Simpson, Bruce Sorrie, Julian Starr, Marcia Waterway, and Laura Young delivered oral presentations on their work. Marccus Alves, Ana Claudia Araújo, Matthew Cimino, Anna Dabros, Sandra Dhooge, Julie Dragon, Jamie Horvath, Philip Hyatt, Chad Kirschbaum, Matthew Palmer, David Simpson, Wayt Thomas, Kathleen Walz, and Vera Williams displayed posters of their work this first day and for the duration of the conference. Keith Clancy, William Crins, Janet Ebert, Bruce Ford, Christopher Frye, Jack Holt, Christopher Lea, William McAvoy, Robert Naczi, Matthew Palmer, Paul Rothrock, and Alfred Schuyler led field trips to see local sedges on the second day. On the third day, Peter Ball, Charles Bryson, William Crins, Bruce Ford, Robert Naczi, Anton Reznicek, Paul Rothrock, and Marcia Waterway led workshops on sedge identification.

The Claude E. Phillips Herbarium of Delaware State University hosted the conference. The Delaware office of the Natural Resources Conservation Service, United States Department of Agriculture (USDA-NRCS); the Society of Natural History of Delaware; and the Delaware Native Plant Society contributed financial support for the conference. In addition, USDA-NRCS contributed substantial financial support for the publication of this book.

Two or three peer reviewers evaluated each manuscript submitted for publication in *Sedges*. All reviewers remained anonymous throughout the review and publication process. We are grateful to the following individuals who generously shared their time and expertise as reviewers: Jerry Baskin, Leo Bruederle, Charles Bryson, Richard Carter, William Crins, Gayle Fritz, Christopher Frye, Rosa Guaglianone, Andrew Hipp, Rod Lastra, James Luken, Gerry Moore, Muthama Muasya, David Murray, Matthew Palmer, Paul Peterson, David Punter, Anton Reznicek, Eric Roalson, Paul Rothrock, David Simpson, Bruce Sorrie, Richard Staniforth, Julian Starr, Mark Strong, Arthur Tucker, Gordon Tucker, Marcia Waterway, and Gerould Wilhelm. David Murray, Gerry Moore, Julian Starr, and Arthur Tucker deserve special recognition for each reviewing two manuscripts. Also, we are thankful to Alan Whittemore for handling the review process for our own manuscript so that all reviews for *Sedges* would be anonymous and as objective as possible.

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Robert F. C. Naczi
Bruce A. Ford

Chapter 1

Frosted Curls to Tiger Nuts: Ethnobotany of Cyperaceae

David A. Simpson

ABSTRACT Although a few Cyperaceae species, such as *Cyperus papyrus* L., have had a long ethnobotanical history, the family has usually been considered of minor economic importance compared to families such as Poaceae. Nevertheless, records from herbarium material and the literature suggest wide-ranging but localized use of Cyperacaeae, particularly among tropical taxa. Data pertaining to use have been assembled, databased, and published in checklist form. Forty-five genera and 499 species or infraspecific taxa have been recorded as having economic or ethnobotanical importance. *Carex* L. and *Cyperus* L. are the two most widely used genera. Thirteen first-level use categories of the Economic Botany Data Collection Standard are recorded for the family, among which animal food, weeds, materials, and environmental uses have the highest number of taxa. *Cyperus esculentus* L. occurs in the largest number of use categories. The categories in which Cyperaceae play a significant role are exemplified.

KEY WORDS Economic, horticulture, sedges, uses, weeds.

The family Cyperaceae presently comprises two subfamilies, Mapanioideae and Cyperoideae (Simpson et al., 2007), with 5387 species in 106 genera (Govaerts et al., 2007). A few species have had a long ethnobotanical history, and among these perhaps the best known is *Cyperus papyrus* L., for which records of use stretch back to early Egyptian times.

From reading some accounts of Cyperaceae, an impression is given that the family has little or no economic significance compared to families such as Poaceae. Mabberley (1987: 166) stated that "they are scarcely palatable to animals, including man, and are of almost negligible economic importance when compared with G(ramineae)." Goetghebeur (1998: 153) commented that the "Cyperaceae are generally of limited economic value and often used locally."

In contrast, Chant (1993: 293) noted that the "family contains a large number of useful species which are employed for a wide variety of uses." This supports my own observations of label data on herbarium specimens and from the literature, confirming that a large number of taxa have had some use, or have had secondary economic importance as weeds of agriculture and horticulture, particularly among tropical taxa. Moreover, archaeological and ethnobotanical evidence suggests that Cyperaceae have been utilized many times in the past. For example, a *Cyperus* L. sp. was listed for its medicinal use in the Ebers Papyrus, itself made from the culms of *C. papyrus*. *Cyperus* was also a major ingredient in kyphi, a fragrance used for embalming, incense, and personal adornment. There are also ancient medicinal uses of *Cyperus* spp. recorded in Middle Eastern literature (Lev, 2002). Moerman (1998), who has documented Native American uses for the family, indicated that ca. 60 taxa had been in use at various times.

Therefore, I was not convinced that the family could be so easily dismissed, as had been suggested by some authors. A more accurate assessment of their importance was needed, which would be quantified by determining the numbers of taxa being used and what they were being used for. To do this, data pertaining to economic, ethnobotanical, or horticultural use were assembled and databased. These were subsequently published in checklist form (Inglis, 1994; Simpson & Inglis, 2001). The aim of this paper is to present an overview of this work and to exemplify the taxa being used together with the types of use in which Cyperaceae play a significant role.

Materials and Methods

Data were assembled from a range of sources including herbarium specimens, economic botany artifacts, field notes, literature, personal communications, and the Internet. Databasing was carried out using the Alice Biodiversity Data Management System Version 2.1 release 14 (Alice Software Partnership, 2005). Data entry conformed to the Economic Botany Data Collection Standard (Cook, 1995). Taxa were initially assigned to one or more first-level use categories defined by the Standard, with further assignment into second-level categories defined by the Standard under each first-level category (Appendix 1). The second-level categories give a more precise indication either of the parts of the plant used (in the case of the food-related categories) or what the plant is used for.

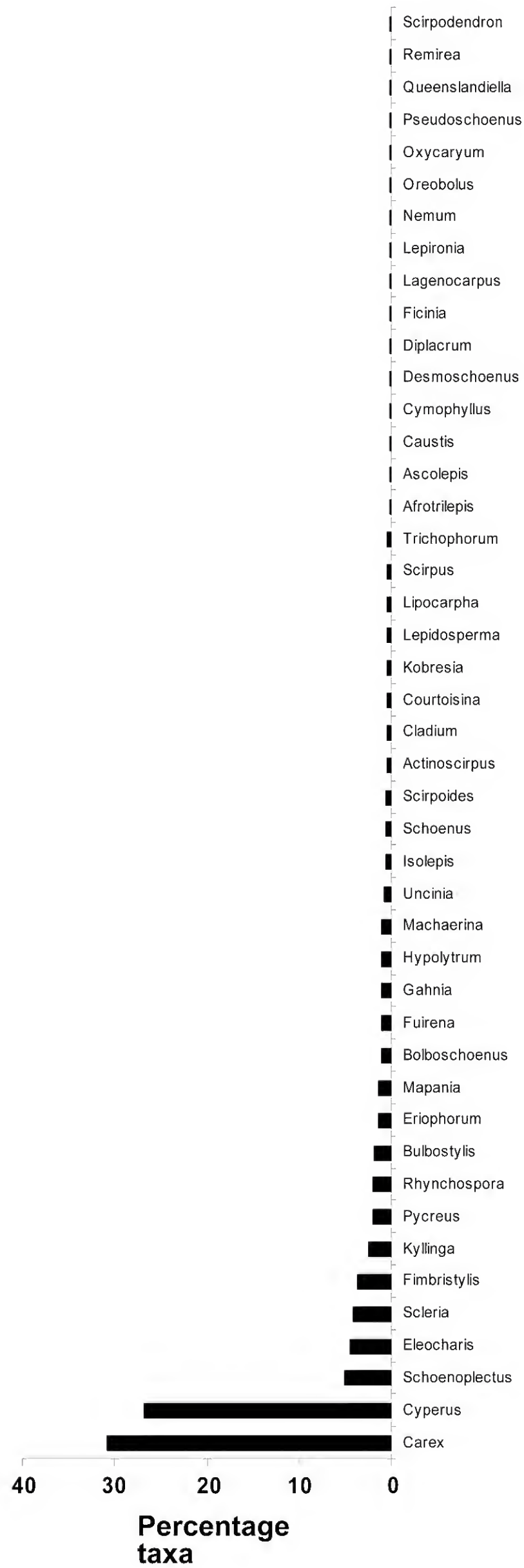
Weeds were included here as an additional first-level category, although they do not form part of the Standard. However, given the large number of Cyperaceae that are recognized as weeds, together with the effects that weedy taxa have on many rural economies, it was felt that this was the most appropriate way of including them in the survey. Second-level categories were devised based on the weed type definitions used in Kühn (1982).

One potential problem when developing the data set was the accuracy of naming, particularly in the older literature, and especially when a taxon had been subject to frequent name changes. Comparison of literature records with herbarium material suggested that much of the naming was correct, and in many cases it was possible to link the uses data to one or more herbarium specimens. Care was taken to ensure that the currently accepted name was applied in the database. Where a name was in doubt and there was no clear way to verify the name being cited with the use, the record was excluded from the data set.

Uses and Examples of Use

General Observations

A total of 45 genera and 499 species or infraspecific taxa were recorded as having economic or ethnobotanical importance. Taxa are used on all



continents (except Antarctica), most extensively so in the tropics (up to 70% of taxa). The data confirm that the taxa are particularly important in local or regional economies, an example being the use of species such as *Cyperus corymbosus* (L.) Rottb. in the local or regional production of basketry and matting in tropical Asia (see the Materials section below).

Figure 1 shows the percentage of taxa of importance grouped by genus. The highest number of taxa are in *Carex* L. (154 taxa [31% of the total number of taxa recorded]) and *Cyperus* (134 [27%]). This may be expected given that they are the two largest genera in Cyperaceae with ca. 2000 and ca. 600 species, respectively. A large drop in the number of taxa is seen between *Cyperus* and *Schoenoplectus* (Rchb.) Palla, the third most-used genus, which has 25 (5%) of the taxa used. Twenty-seven genera have three or fewer taxa included.

Thirteen first-level use categories were recognized for Cyperaceae (Appendix 1). Figure 2 shows the percentage of taxa allocated to each of these categories. The greatest number (180 taxa [21% of the total number of taxa recorded]) occur in the Animal Food category, followed by Weeds (168 [20%]), Materials (142 [17%]), and Environmental Uses (141 [17%]).

Figure 3 shows the taxa that occur in the highest number of first-level use categories. The top four are *Cyperus esculentus* L. (12 categories), *C. papyrus* (10), *C. articulatus* L. (9), and *C. alternifolius* L. (8). These and other important taxa also

Figure 1. Percentage of taxa of economic or ethnobotanical importance grouped by genus. Authorities are provided for the following genera that are cited here for the first time in the paper: *Scirpodendron* Zipp. ex Kurz, *Remirea* Aubl., *Queenslandiella* Domin, *Pseudoschoenus* (C. B. Clarke) Oteng-Yeboah, *Oxycaryum* Nees, *Oreobolus* R. Br., *Nemum* Desv., *Lepironia* Rich., *Lagenocarpus* Nees, *Ficinia* Schrad., *Diplacrum* R. Br., *Desmoschoenus* Hook. f., *Cymophyllus* Mack., *Caustis* R. Br., *Ascolepis* Nees ex Steud., *Afrotrilepis* (Gilly) J. Raynal, *Trichophorum* Pers., *Scirpus* L., *Lipocarpha* R. Br., *Lepidosperma* Labill., *Courtoisina* Soják, *Cladium* P. Browne, *Actinoscirpus* (Ohwi) R. W. Haines & Lye, *Scirpoides* Ség., *Schoenus* L., *Isolepis* R. Br., *Machaerina* Vahl, *Hypolytrum* Rich., *Gahnia* J. R. Forst. & G. Forst., *Mapania* Aubl., and *Bulbostylis* Kunth.

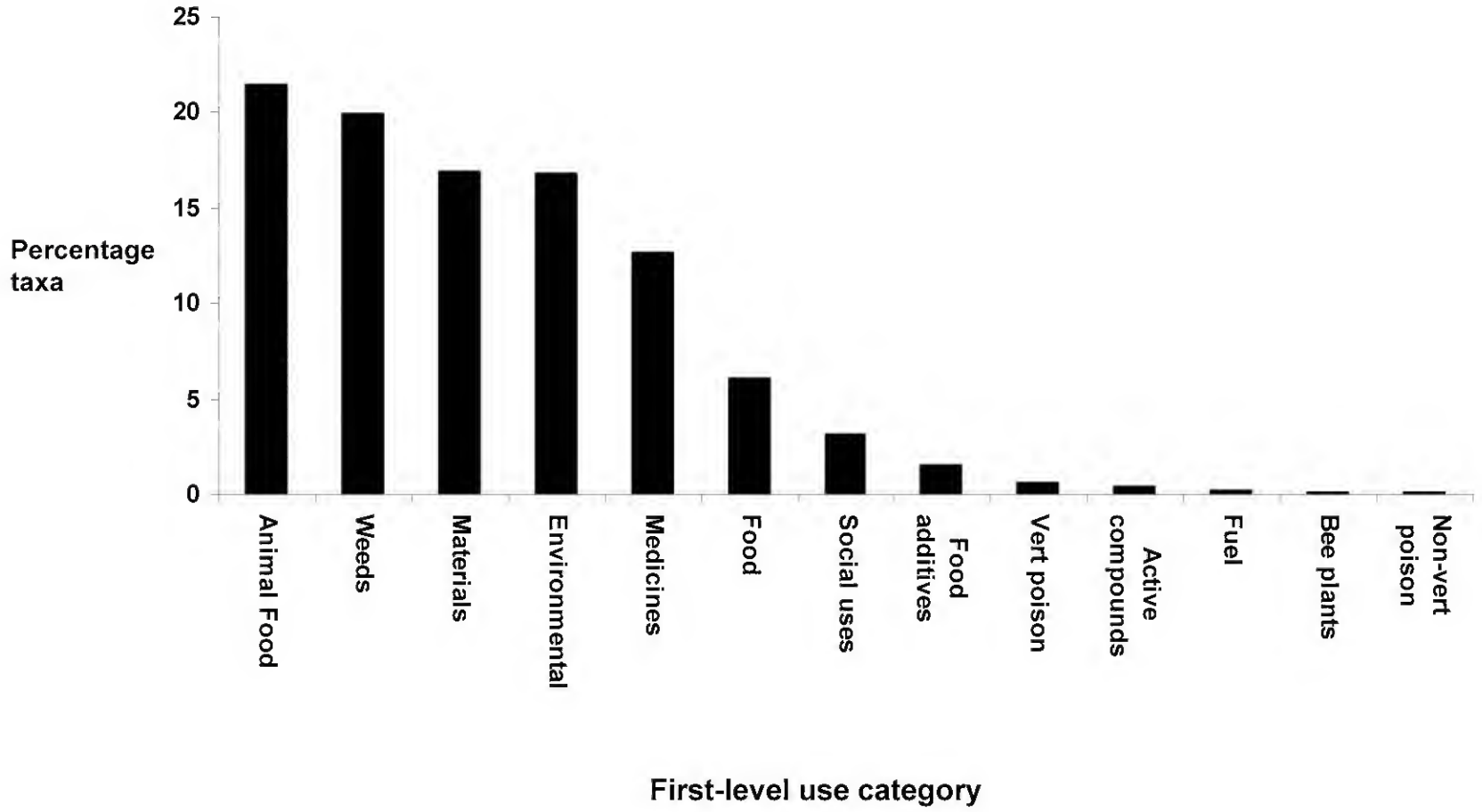


Figure 2. Percentage of taxa of economic or ethnobotanical importance grouped by first-level use category.

have widespread distributions that may be partly due to human activity. For example, *C. papyrus*, which is native to northern and eastern Africa, has been introduced to southern Europe, tropical Asia, and tropical South America, while *C. alternifolius*, native to tropical Africa, has been widely introduced elsewhere. In both cases, their use as ornamental plants has probably brought about extensions to their natural range. Also, many common rice field weeds such as *Cyperus difformis* L. and *Fimbristylis dichotoma* (L.) Vahl have pantropical distributions that may have been accentuated through the spread of rice as a crop.

ANIMAL FOOD

As suggested by Mabberley (1987), Cyperaceae are often considered to be unpalatable to animals, and therefore rank very poorly as a food source compared to Poaceae. However, in the present work 20 genera and 178 species/infraspecific taxa were found to have importance as animal food (Fig. 4). Of these, the greatest prominence is given to *Carex*, with 80 (45%) of the taxa in this category. Most of these (71 taxa) were documented by Hermann (1970) for their importance as grazing for cattle, sheep, and horses in the United States. Within the same tribe, *Kobresia pygmaea* (C. B. Clarke) C. B. Clarke was considered by Dickoré (1994: 83) as "the most important plant of Tibet, highly adapted and tolerant to grazing." He also noted that "it appears to be a main fodder-plant and that its distribution coincides with the area of large-scale yak-pasturing." Noltie (1994) also observed the importance of *Kobresia* Willd. for grazing by yak and sheep in Bhutan.

Cyperus also figures prominently in this category, representing 52 (29%) of the taxa. Many of these are African or Asian taxa that offer poor to moderate value grazing for livestock. For example, *Cyperus distans* L. f. is recorded from herbarium material as being grazed by cattle, goats, and sheep (Simpson & Inglis, 2001), while *C. alternifolius* is grazed by all domestic livestock (Burkill, 1985).

The remaining 18 genera in this category include *Kyllinga* Rottb. (7 taxa [4%]), *Rhynchospora* Vahl (6 [3%]), *Eleocharis* R. Br. (4 [2%]), and *Schoenoplectus* (4 [2%]). Among these, *Kyllinga nemoralis* (J. R. Forst. & G. Forst.) Dandy ex Hutch. & Dalziel is used for grazing in Southeast Asia when little grass is available (Burkill, 1935; Kern, 1974).

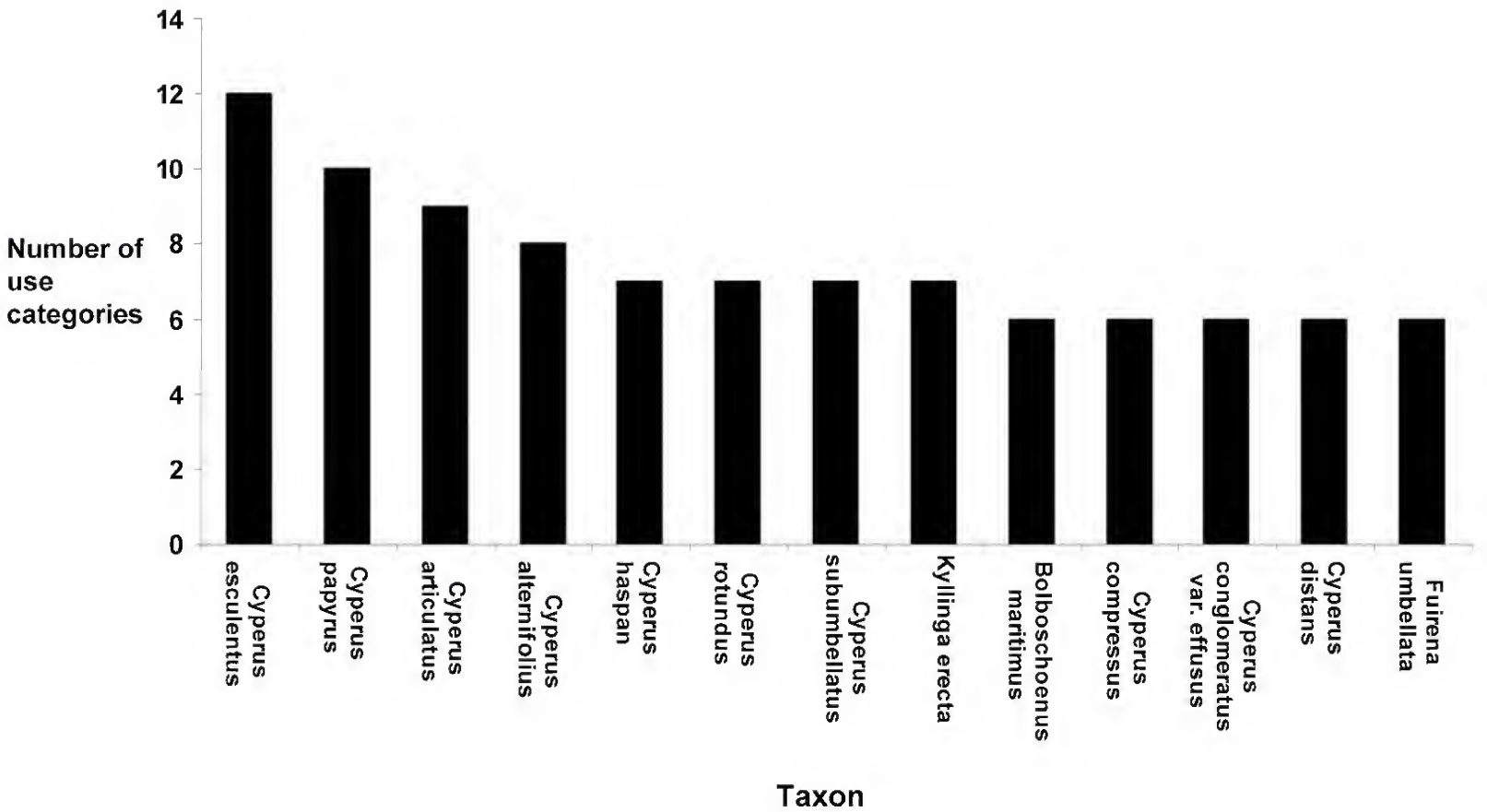


Figure 3. Taxa occurring in the greatest number of first-level use categories. Authorities are provided for the following taxa that are cited here for the first time in the paper: *Cyperus conglomeratus* var. *effusus* (Rottb.) Kük. and *Cyperus compressus* L.

WEEDS

A comprehensive analysis of weedy Cyperaceae has been undertaken by Bryson and Carter (2008). In the work presented here, 21 genera and 168 species/infraspecific taxa were assigned to the "Weeds" category (Fig. 4). The importance of Cyperaceae as weeds cannot be overstated. One species, *Cyperus rotundus* L., is described as the world's worst weed (Holm et al., 1977) and the Guinness Book of Records (Mathews, 1996) described it as the world's most damaging weed. Terry (2001) noted three other species as being particularly serious, namely *C. difformis*, *C. esculentus*, and *C. iria* L. He attributed the success of these taxa to a number of shared characteristics, including their reproductive efficiency, rapid growth and maturation, an ability to grow in a wide range of habitats, an ability to aggressively compete for light, nutrients, and water, and their resistance to control.

The weedy taxa predominantly occur in *Cyperus*, with 78 (46%) of the taxa in this category. The next most weedy genera are *Carex* (19 [11%]), *Eleocharis* (12 [7%]), and *Fimbristylis* Vahl (12 [7%]). Terry (2001) noted a similar pattern based on the frequency of citations of the genera in the literature on weeds between 1973 and 2001.

Many of the weed taxa are pantropical, and their extensive distributions may be at least partly due to human activities. The top five tropical weed species, based on the number of occurrences in second-level categories, are *Cyperus rotundus*, *C. esculentus*, *C. iria*, *C. haspan* L., and *Fimbristylis dichotoma*. They are problematic throughout the tropics.

The problems caused by weedy Cyperaceae are amply demonstrated by *Cyperus rotundus*. This species is a weed of 52 crops in 92 countries (Parsons & Cuthbertson, 1992; Bromilow, 1995), mostly in the tropics and subtropics. It is a particular problem in sugar cane, rice, cotton, maize, and other major crops. It spreads mainly through the dispersal of its underground rhizomes and tubers. In dense colonies, 500 plants per square meter have been observed and 53,000 tubers have been recorded per cubic meter of soil (Parsons & Cuthbertson, 1992). Moreover, it is resistant to many herbicides (Bromilow, 1995). As a result, it costs millions of dollars per year in control and lost production.

Despite being serious weeds, many such taxa are also widely used. For example, *Cyperus rotundus* occurs in five first-level use categories including Food and Environmental Uses (as a soil binder: Parsons & Cuthbertson, 1992), while *C. esculentus* occurs in eight categories, again including food (see the Food section below) and materials. The top five weedy species also have medicinal uses. This applies notably to *C. rotundus*, whose rhizomes are an important part of Chinese herbal medicine (see the Medicines section below).

MATERIALS

Thirty genera and 142 species/infraspecific taxa fall within this category (Fig. 4). *Cyperus* is the most widely used genus, representing 59 (42%) of the taxa in the category, followed by *Schoenoplectus* (12 [8%]), *Eleocharis* (10 [7%]), *Scleria* P. J. Bergius (7 [5%]), and *Carex* (6 [4%]). A wide range of uses occurs in this category, from boat building, construction, and roofing, to basketry, matting, clothing, papermaking, and perfumery.

Among the most versatile of the taxa in this category is *Cyperus papyrus*, which provides material for boat building, matting, mattressing, roofing, rope work, and small-scale fiberboard production. It is also well known as the raw material for papyrus. This is still manufactured on a small scale today, mainly for use in tourist souvenirs. Related to this, there have been attempts to make paper from several other Cyperaceae, including *C. esculentus* and *Lepidosperma gladiatum* Labill. (Anon., 1988; Simpson & Inglis, 2001), although none of these have been developed on a large scale.

A few other taxa are employed for boat building. These include *Schoenoplectus tatora* (Kunth) Palla, which is well known as the plant that grows around Lake Titicaca in Peru and is used by the Uros and Aymar Indians to construct canoes and rafts (Lewington, 1990). On the coast of Peru, *S. riparius* (C. Presl) Palla is put to similar use (Lewington, 1990).

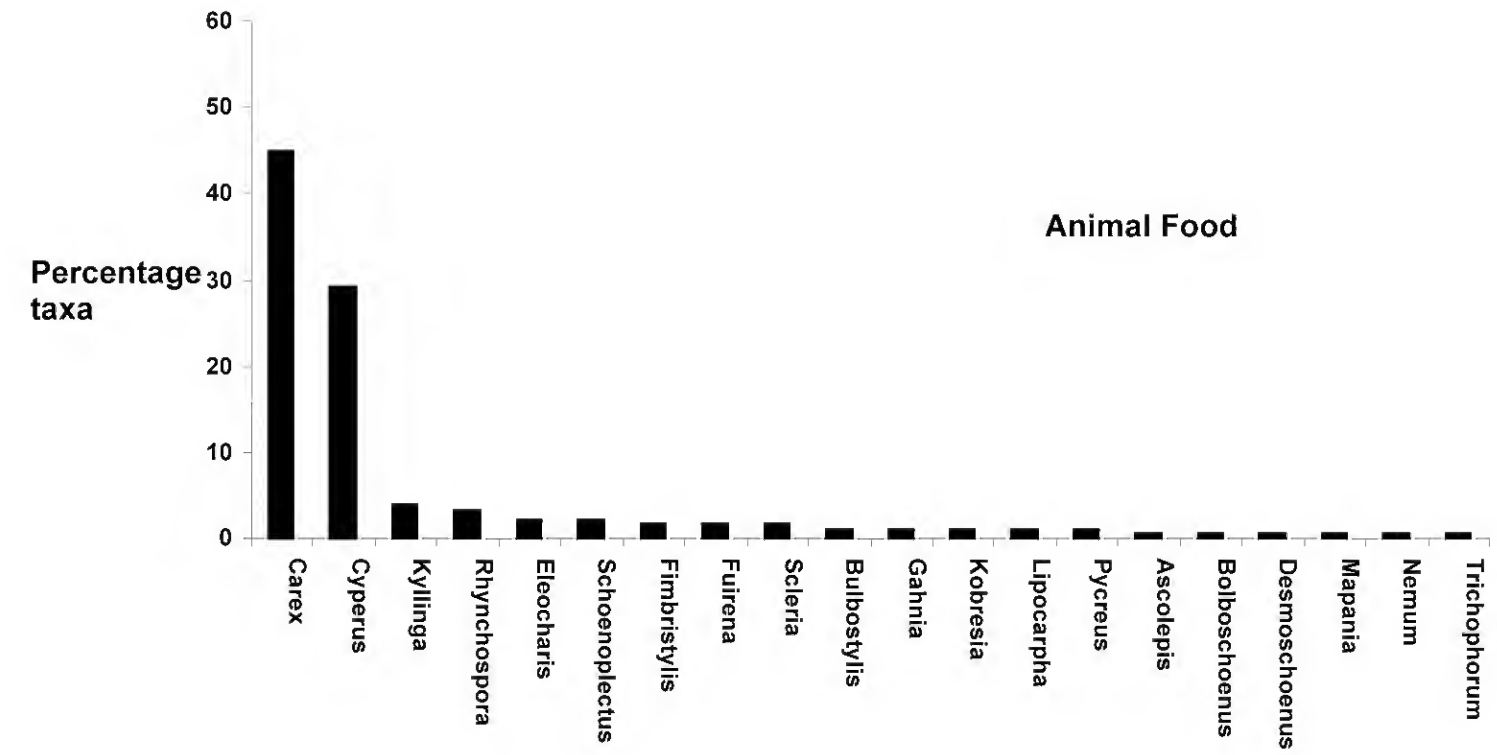
Some taxa are used in building construction. Several are used for thatching, such as *Afrotrilepis pilosa* (Boeck.) J. Raynal, *Cladium mariscus* (L.) Pohl, and *Scleria depressa* (C. B. Clarke) Nelmes, while *Scleria poaeformis* Retz. is used for making roof tiles to cover huts and outbuildings in parts of northeastern Thailand (D. A. Simpson, pers. obs.). At least two species are used for the construction of whole buildings. Sods of *Kobresia pygmaea* turf are used in Tibet to build both walls and roofs of houses (Dickoré, 1994), and in South Africa, the culms of *Cyperus textilis* Thunb. are used in the construction of traditional beehive huts (Van Eyk & Gericke, 2000).

A large number of sedges are used for basketry and matting. Among these, *Cyperus alternifolius* is widely employed for making items such as baskets, plates, and covered containers in eastern and northeastern Africa (Tredgold, 1986; Simpson & Inglis, 2001) (Fig. 5A, B), while *Lepidosperma gladiatum* has similar uses in parts of Australia (Simpson & Inglis, 2001). *Lepironia articulata* (Retz.) Domin, widely used for basketry and matting in Southeast Asia (Kern, 1974; Simpson & Koyama, 1998) and Madagascar, is sometimes cultivated. Its occurrence in Madagascar is well away from the main area of distribution in tropical Asia. Although speculative, it is possible that the plant was brought to the island by the people who migrated there from Southeast Asia ca. 1000–2000 years ago.

A number of taxa have aromatic rhizomes containing essential oils, for example *Cyperus articulatus* L. and *C. rotundus*. Both of these are used in perfumery (Burkill, 1985; Abbiw, 1990; Chant, 1993), and also as an insect repellent (Burkill, 1985; Millar & Morris, 1988). Burkill noted that *C. articulatus* is cultivated for its rhizomes in western Africa.

Some taxa in this category are recognized for their importance as contributors to rural economies especially in the tropics and subtropics. *Cyperus textilis* and *C. sexangularis* Nees, both close relatives of *C. alternifolius*, are used in South Africa to make a wide range of products, including sleeping and work mats, traditional house construction, collecting and winnowing baskets, rolled twine, and cutting boards (Burkill, 1935; Kükenthal, 1935–1936; Van Eyk & Gericke, 2000). Although generally harvested from the wild, they are sometimes planted in rice paddies. The finished goods are marketed throughout South Africa as well as exported, and provide a useful source of income to rural communities, particularly in Kwazulu-Natal Province.

Cyperus corymbosus is similarly important in parts of southern India and northeastern Thailand (Amalraj, 1991; Simpson, 1992a, pers. obs.).



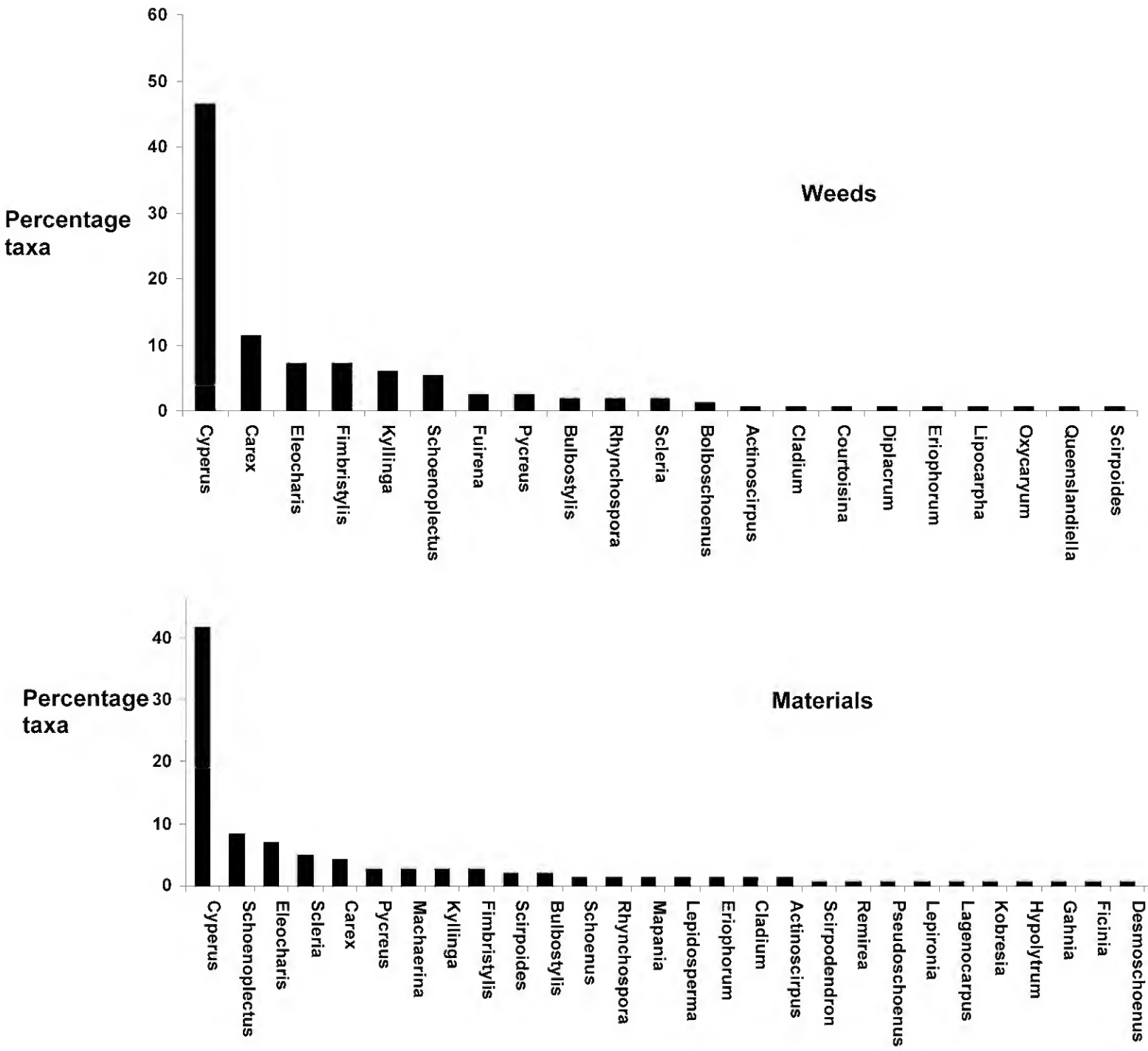


Figure 4. Percentage of taxa of economic or ethnobotanical importance grouped by genus, for three first-level use categories: Animal Food, Weeds, and Materials.

The plant is often cultivated on the margins of rice paddies, and the dried culms are dyed and woven into floor mats, table mats, basketry, and various other items. These are sold widely in the respective countries, but there is also a significant export of the products, particularly to other parts of Asia and Europe. While most of the products are woven by hand, there have been some attempts to mechanize the production of matting in India through the development of a semi-automatic loom. Other species are used, including *C. pangorei* Rottb. in India and *Actinoscirpus grossus* (L. f.) Goetgh. & D. A. Simpson in Thailand. However, they are generally inferior in quality to *C. corymbosus*.

Among a range of other uses in this category, *Cyperus esculentus* has been employed in soap making (Burkill, 1985) and in the production of lubricating oil for watches (Tackholm & Drar, 1950); *Eriophorum vaginatum* L. has been used to make yarn and cloth in the United Kingdom (Simpson & Inglis, 2001); *Schoenoplectus lacustris* (L.) Palla has been used to make protective sleeve cuffs in the United Kingdom (Fig. 5C); and an *Eleocharis* sp. has been used to make pack saddles in Argentina (Fig. 5D) (Simpson & Inglis, 2001).

ENVIRONMENTAL USES

Twenty-six genera and 140 species/infraspecific taxa are in this category (Fig. 6). *Carex* has the largest representation, accounting for 55 (39% of the taxa), followed by *Cyperus* (33 [24%]), *Fimbristylis* (7 [5%]), and *Eleocharis* (6 [4%]). Many of the taxa in this category are ornamentals. Fifty-one *Carex* taxa were recorded as having horticultural uses and the list is increasing, with new taxa appearing in trade fairly regularly. Other genera with taxa of horticultural interest include *Cyperus*, *Eriophorum* L., *Schoenoplectus*, and *Uncinia* Pers. Cyperaceae form an important part of what are known in horticulture as "ornamental grasses." These plants are grown mainly for their foliage characteristics. A few taxa are also used in floristry, in particular *Caustis dioica* R. Br. (frosted curls), of which both fresh and dried material is used.

As with many plants in cultivation, the naming of the taxa can be confusing. For example, in the United Kingdom, *Cyperus subumbellatus* Kük. is sold as an indoor plant under the name "Cyperus sumula," while *Cyperus prolifer* L. is often referred to as *Cyperus papyrus* 'nanus' or "Cyperus haspan." The latter has been confused with *C. haspan*, a pantropical weedy species that is distinct from *C. prolifer* (Simpson, 1994).

Also within the "Environmental Uses" category are taxa that serve as erosion controllers. Plants with extensive networks of rhizomes that grow in predominantly sandy habitats and can withstand long dry periods are regarded as suitable here. They include *Cyperus conglomeratus* Rottb., *C. capitatus* Vand., *C. chordorrhizus* Chiov., and *Remirea maritima* Aubl. *Cyperus conglomeratus* has been widely used in sand-binding, dune stabilization, and ground cover in Saudi Arabia (Burkill, 1985; Al-Zoghet, 1989), while the other taxa are often used in coastal areas for dune stabilization (Simpson & Inglis, 2001). Also useful is *Fuirena umbellata* Rottb., which acts as a mud-binder to reduce coastal erosion (Burkill, 1985).

Some taxa are also useful as revegetators. *Carex filifolia* Nutt. var. *erostrata* Kük. is used for restoring vegetation on gravel areas in montane regions of the United States (Ratliff & Westfall, 1992), while *Cyperus chordorrhizus* is a pioneer species on cemented sands in Somalia (Fagotto, 1987). Fosberg (1988) noted that *Fimbristylis cymosa* covered and stabilized "raw" surfaces on the Bikini Atoll, while *Desmoschoenus spiralis* (A. Rich.) Hook. f. is used as a stabilizer and revegetator after sand-mining on the New Zealand coast. A few taxa are regarded as soil improvers, for example *Actinoscirpus grossus* and *Fimbristylis dichotoma*, both of which are plowed into soil as green manure (Burkill, 1935; Burkill, 1985).

MEDICINES

Eighteen genera and 107 species/infraspecific taxa occur in this category (Fig. 6). *Cyperus* dominates the category with 40 (37%) of the taxa followed by *Scleria* (14 [13%]), *Fimbristylis* (9 [8%]), and *Carex* (7 [7%]). The second-level categories outlined in Appendix 1 give a broad indication of the range of disorders that can be treated with Cyperaceae.

Two *Cyperus* species are regularly used medicinally. As indicated above, *C. rotundus* (especially the rhizome) is important in Chinese medicine (Fig. 5E), and is considered to be diaphoretic, diuretic, hypotensive, and inflammatory, due to the presence

Figure 5. —A, B. Basketry made from *Cyperus alternifolius*, Ethiopia. —C. Protective sleeve cuffs made from *Schoenoplectus lacustris*, United Kingdom. —D. Pack saddles made from *Eleocharis* sp., Argentina. —E. Rhizomes of *Cyperus rotundus*, Sri Lanka. —F. *Cyperus esculentus* tubers marketed as "tiger nuts," United Kingdom. Photographs by Andrew McRobb.

of cyperone (Saralamp et al., 1996). The plant is used to treat a large number of problems, from stomach/bowel disorders (Chin & Keng, 1992; Jain, 1992) and menstrual disorders (Millar & Morris, 1998), to pain relief (Burkill, 1935) and the removal of lice (Deokule & Magdum, 1992). *Cyperus articulatus* is used to treat a similar range of problems. Interestingly, both these species are also reported to have antimalarial properties (Burkill, 1985; Saralamp et al., 1996), and *C. rotundus* has been shown to inhibit the growth of *Plasmodium falciparium* Welch in vitro (Saralamp et al., 1996).

Among the *Scleria* taxa used in this category, most are involved in relief of pain, such as toothache or pain in childbirth. Several species, including *S. boivinii* Steud. and *S. depressa*, are used to treat sexually transmitted diseases.

Other taxa used medicinally include *Bolboschoenus yagara* (Ohwi) Y. C. Yang & M. Zhan, the rhizomes of which are used to treat blood clotting in Chinese medicine (Simpson & Inglis, 2001); *Kyllinga brevifolia* Rottb., the leaves of which are used to treat stomach and intestinal disorders in India (Kapur et al., 1992; Mukhopadhyay & Ghosh, 1992); *Hypolytrum purpurascens* Cherm., of which a decoction of leaves is used to make a cough medicine in Sierra Leone (Burkill, 1985); and *Carex nivalis* Boott, from which the leaves are powdered and made into a paste that is applied as an antiseptic on open wounds (Navchoo & Buth, 1992).

Although the scientific basis for many of these remedies has not been tested, the widespread use of some taxa suggests they have useful properties that should be investigated further.

FOOD

Cyperaceae have long played an important role, with 15 genera and ca. 55 taxa recorded as food plants (Fig. 6). The most commonly used genus is *Cyperus*, representing 27 (53%) of the taxa used for food. Other genera here include *Schoenoplectus* (6 [12%]), *Bolboschoenus* (Asch.) Palla (3 [6%]), and *Eleocharis* (2 [4%]). Rhizomatous and tuberous taxa are most often used and it is the underground parts that are eaten. They are often regarded as a famine food.

Of the taxa in this category, *Cyperus esculentus* and *Eleocharis dulcis* (Burm. f.) Trin. ex Hensch. are probably the most important and well known. The tubers of *C. esculentus* are sold raw as "tiger nuts" (Fig. 5F) or are crushed and made into a soft drink known as "horchatas de chufa" (Burkill, 1985; Anon., 1988). The latter is very popular in Spain where the plant is widely cultivated, with a number of cultivars being developed. They may also be used as a coffee or almond substitute and have been made into a caffeine-free "chocolate" (Burkill, 1985).

Eleocharis dulcis var. *tuberosa* (Roxb.) T. Koyama (Chinese water chestnut) is a widespread crop in tropical and warm-temperate Asia that is also cultivated on a very minor scale in the United States and Australia. The tubers are large and fleshy, and can be eaten raw or cooked. They are exported worldwide, either fresh or canned.

Among the lesser-known food taxa, very young plants of *Scleria biflora* Roxb. are fragrant and eaten raw or steamed with rice in parts of Indonesia (Kern, 1974), while *Cyperus bulbosus* Vahl produces small tubers that are eaten roasted or boiled in various parts of the Old World tropics (Kükenthal, 1935–1936; Simpson & Inglis, 2001). The nutlets of a few species are eaten, including *Bolboschoenus paludosus* (A. Nelson) Soó (Anon., 1994–2000) and *Scirpodendron ghaeri* (Gaertn.) Merr. (Kern, 1974).

SOCIAL USES

This category includes eight genera and 26 taxa, of which *Cyperus* (17 taxa [65% of the taxa used in the category]) forms the largest group.

A few taxa are said to have hallucinogenic properties. For example, in Peru the leaves and rhizomes of *Cyperus prolixus* Kunth are mixed with tobacco and smoked to give the desired effect.

Most of the taxa in this category are used for ritual or ceremony. *Cyperus articulatus* in particular is widely used in ritual in Africa and South America. It is used to counteract witchcraft in Ecuador (Plowman et al., 1990) and is employed by the Shipibo-Conibo in Peru in ritual ceremonies to encourage better hunting and fishing (Tournon et al., 1986). In Nigeria the rhizome is chewed by a defendant in court as a charm to secure acquittal (Burkill, 1985) and may also be used to ensure success in trade and to ward off evil spirits (Burkill, 1985).

Other taxa used include *Afrotrilepis pilosa* in Ivory Coast, which is said to ward off lightning from buildings (Burkill, 1985), and in Madagascar *Cyperus esculentus* is considered to have aphrodisiac properties (Cauis & Banby, 1935).

FOOD ADDITIVES

Thirteen taxa in four genera are used as food additives. *Cyperus* comprises seven (54%) of the taxa in this category, followed by *Kyllinga* (4 [31%]), *Fuirena* Rottb. (1 [8%]), and *Pycreus* P. Beauv. (1 [8%]). Most of the taxa are used as a salt substitute in parts of Africa, the plants being burnt and the resultant ash added to food (Burkill,

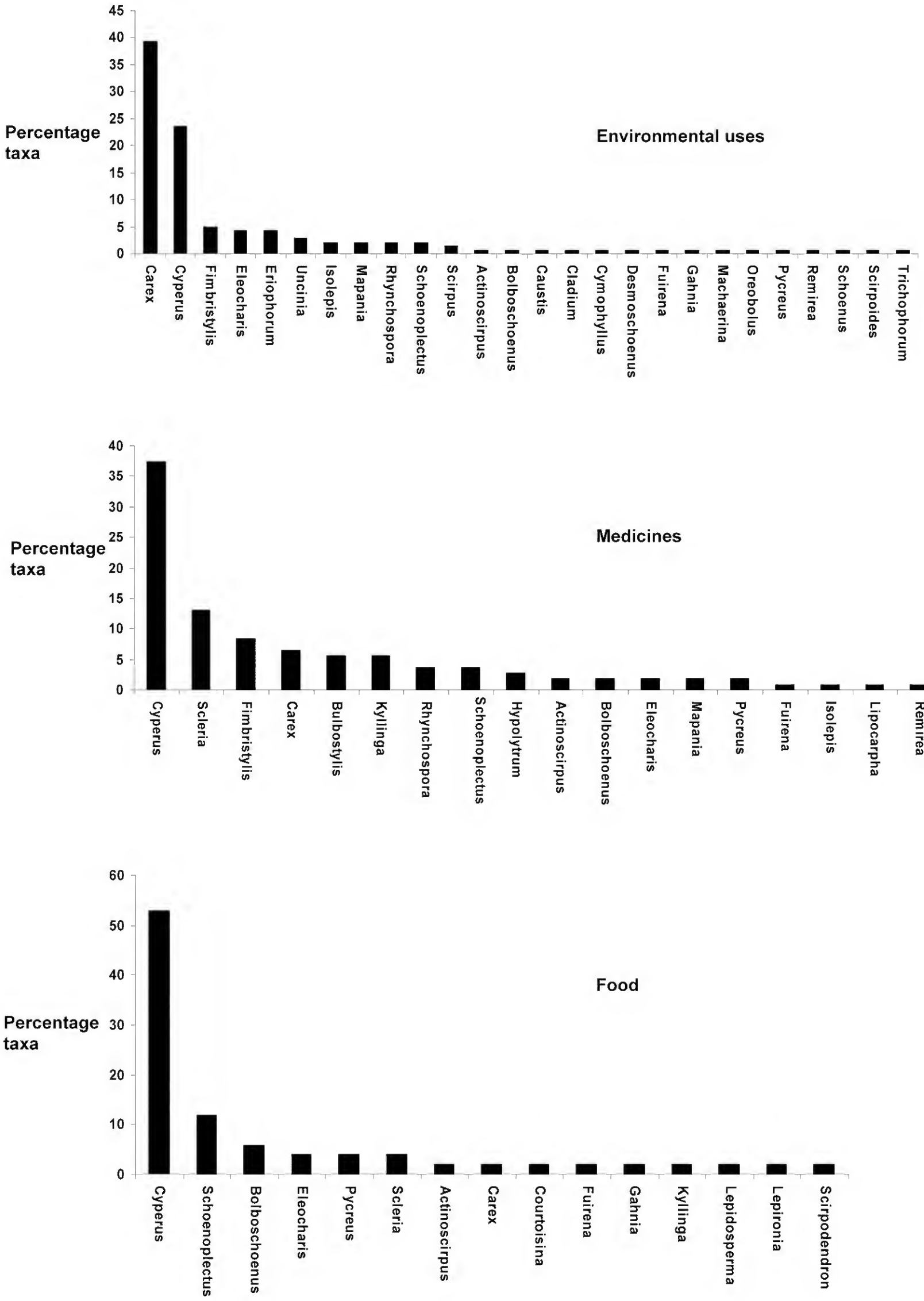


Figure 6. Percentage of taxa of economic or ethnobotanical importance grouped by genus, for three first-level use categories: Environmental Uses, Medicines, and Food.

1985; Abbiw, 1990). *Kyllinga erecta* Schumach., *K. pumila* Michx., and *K. squamulata* Thonn. ex Vahl are used as a food flavoring, again in Africa (Burkill, 1985; Abbiw, 1990).

VERTEBRATE POISONS

Carex cernua Boott and *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J. Raynal have been reported to be poisonous to cattle (Cauis & Banby, 1935), while *Pycreus nitidus* (Lam.) J. Raynal is suspected to cause "vlei" disease in sheep in South Africa (Burkill, 1985).

ACTIVE COMPOUNDS PRESENT

Three taxa, *Bolboschoenus maritimus* (L.) Palla, *Cladium mariscus* subsp. *jamaicense* (Crantz) Kük., and *Cyperus alternifolius*, are reported to contain alkaloids (Burkill, 1985).

FUEL

Cyperus papyrus is used as a fuel in Uganda and Rwanda (Jones, 1983). In Rwanda, a pilot factory was set up in the 1980s to process culms into fuel briquettes, although this was abandoned after the political troubles in 1994 (M. B. Jones, pers. comm.).

BEE PLANTS

Several taxa are reported to be visited by bees, including *Carex* spp. (Leppik, 1955), *Cymophyllus fraserianus* (Ker Gawl.) Kartesz & Gandhi (Thomas, 1984), *Cyperus esculentus* (Burkill, 1985), *Rhynchospora* spp. (Thomas, 1984), and *Mapania* spp. (Simpson, 1992b).

NON-VERTEBRATE POISONS

Cyperus cyperoides (L.) Kuntze is used as a vermifuge in Sumatra (Chant, 1993), while *C. rotundus* and *Schoenoplectus senegalensis* (Hochst. ex Steud.) Palla ex J. Raynal are used as molluscicides in parts of Africa (Ahmed et al., 1984; Anon., 1994–2000).

CONCLUSIONS

The present study has served to highlight both the numbers of Cyperaceae taxa used and the range of uses to which they are put. Their importance is much greater than previously thought, and new uses of taxa or new taxa being used come to light fairly regularly, so there is still information gathering to be done. The potential for promoting other aspects of use, for example basketry/matting, medicines, and perhaps biofuel, is considerable, and it will be interesting to monitor future developments.

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Appendix 1

First- and second-level Use Categories for Cyperaceae following Cook (1995). Weeds are included here as an additional category.

Food
Unspecified part; entire plant; aerial parts; tubers; rhizomes; culms; leaves; nutlets

Food additives
Unspecified part; entire plant; rhizomes; culms; exudates

Animal food
Unspecified part; tubers; rhizomes; leaves/culms/aerial parts; inflorescences/infructescences/nutlets

Bee plants
Inflorescence

Materials
Unspecified material type; fibers; cane/reed; other materials/chemicals

Fuels
Miscellaneous fuels; tinder

Social uses
Smoking materials and drugs; antifertility agents; "religious uses"; miscellaneous social uses

Vertebrate poisons
Mammals

Non-vertebrate poisons
Mollusca

Medicines
Unspecified medicinal disorders; blood system disorders; circulatory system disorders; digestive system disorders; endocrine system disorders; genito-urinary system disorders; ill-defined symptoms; infections/infestations; inflammation; injuries; metabolic system disorders; mental disorders; muscular-skeletal system disorders; nervous system disorders; nutritional disorders; pain; poisonings; pregnancy/birth/puerperium disorders; respiratory system disorders; sensory system disorders; skin/subcutaneous cellular tissue disorders

Environmental uses
Unspecified environmental uses; erosion control; revegetators; soil improvers; ornamentals

Weeds
Unspecified weed; cultivation; rotation crops; perennial crops; grassland; waste places; disturbed land; aquatic biotopes; rice fields; irrigation ditches; gardens; pasture; forests

Active compounds present
Alkaloids

Chapter 2

The Significance of Cyperaceae as Weeds

Charles T. Bryson and Richard Carter

ABSTRACT Weedy Cyperaceae adversely affect natural plant communities and the health of humans and livestock and are major deterrents to agricultural and forest productivity. Most weeds are exogenous and have traits that give them biological and reproductive advantages over other plants. Weeds cost billions of dollars in agriculture, forestry, and urban areas and threaten diversity in natural communities worldwide. Of an estimated 8000 species of weeds worldwide, only about 200 species cause approximately 95% of the problems in production of food, feed, fiber, and livestock. About 25% of the world's weeds are monocots. Of these, sedges are among the most troublesome and difficult to control. The most important cyperaceous weeds in terms of their adverse effect on agriculture include *Cyperus rotundus* L., *C. esculentus* L., *C. difformis* L., *C. iria* L., and the *Fimbristylis miliacea* (L.) Vahl/*F. dichotoma* (L.) Vahl complex, ranking first, 16th, 32nd, 33rd, and 40th among the world's worst weeds, respectively. We provide an overview of cyperaceous weeds, including economic losses, population dynamics, control methods, identification, biology, ecology, dispersal mechanisms, spread, and discussions of major weeds of agriculture, forestry, urban areas, and natural communities.

KEY WORDS *Abildgaardia*, *Bolboschoenus*, *Bulbostylis*, *Carex*, *Cladium*, *Courtoisina*, *Cyperaceae*, *Cyperus*, *Eleocharis*, *Fimbristylis*, *Fuirena*, *Isolepis*, *Kyllinga*, *Lepidosperma*, *Lepironia*, *Lipocarpha*, *Mapania*, *Oxycaryum*, *Rhynchospora*, *Schoenoplectus*, *Scirpodendron*, *Scirpus*, *Scleria*, sedge, weed.

Cyperaceae is a cosmopolitan family with ca. 5000 species and 100 genera (Ball et al., 2002). Members of Cyperaceae, commonly called sedges, are monocot flowering plants with reduced, mostly wind-pollinated (anemophilous) flowers. The inconspicuous flowers are organized into spikelets, and the spikelets further arranged into higher order spicate, paniculate, or umbellate inflorescences. Flowers may be either perfect or imperfect, and when imperfect, plants are monoecious (or rarely dioecious). Fruits are small single-seeded achenes. Sedges are primarily grass-like herbs with linear leaves and parallel venation. Cyperaceae and Poaceae have traditionally been treated as related families (Cronquist, 1981). Recent cladistic analysis using molecular and morphological data confirms a closer relationship with Juncaceae, with the "sedge clade" consisting of Cyperaceae, Juncaceae, and Thurniaceae (Chase et al., 2000).

Many species of Cyperaceae are heliophytes, adapted to open, sunny areas with reduced competition from taller shading trees and shrubs. Such habitats are often dependent upon natural or artificial disturbance. A variety of plants, including many sedges, have intrinsic characteristics (e.g., high reproductive output, rapid growth, vegetative proliferation, extended seed dormancy) that promote population expansion after disturbance and probably originally evolved as colonizers of disturbed habitats (Baker, 1965, 1974; McNaughton & Wolf, 1973). In addition to catastrophic disturbances, more subtle and continual natural processes provide open areas for colonization by such species, e.g., exposed bars and banks along streams and coasts (Baker, 1974).

Plants are often called weeds when they opportunistically colonize and occupy habitats artificially disrupted and maintained by humans, e.g., agricultural fields, lawns, and gardens (Baker, 1974). The term "weed" is inherently anthropocentric and, therefore, is fundamentally problematic when used in science. Some definitions are entirely subjective and consequently are of little use in science, e.g., "a plant growing out of place" (James et al., 1991: 1) or "a plant growing where it is not desired" (Buchholtz, 1967: 389), and others emphasize only the negative effects of weeds on natural communities and ecosystems (Zimdahl, 1995; Randall, 1997). Although the latter are applicable to natural resource management and basic ecology, they are too restrictive for broader application to agriculture and other applied sciences. Bryson (2003: 1571) defined a weed as "an undesirable plant that adversely affects humans or other organisms which humans deem desirable." Reducing further the anthropocentric emphasis and incorporating elements applicable in both pure and applied sciences, we propose the following definition: *Weeds are plants that alter the structure of natural communities, interfere with the function of ecosystems, or have negative effects on humans, agriculture, or other societal interests.*

Cronk and Fuller (1995) clearly distinguish between invasive plants that invade natural areas and weeds or ruderals that infest agricultural or other highly disturbed, artificial habitats, and they provide a system of ranking weeds and invasive plants. The same characteristics that enable plants to colonize an area during ecological succession can make them invasive pests when they are introduced outside their natural ranges or habitats. Invasive weeds alter wildlife habitat by reducing quantity and quality of food sources, nesting sites, and cover, by increasing the frequency of fire and soil erosion, and by changing the natural dynamics of aquatic systems causing flooding or desiccation. Contrastingly, in agriculture the most important weeds are those that have the greatest economic impact through reduction in crop yield, interference, or reduced efficiency or quality of harvest.

About 8000 species, or approximately 3% of the total number of plant species worldwide, have been documented as weeds (Holm et al., 1977). Of these, about 200 species, less than 0.1% of the world's flora, account for approximately 95% of weed problems in agriculture (Holm et al., 1977, 1979, 1997). Invasive weeds possess a variety of characteristics enabling them to disperse rapidly into new areas and outcompete crops or native or desirable non-native vegetation for light, water, nutrients, and space (Westbrooks, 1998). To varying degrees, many characteristics contribute to the success and competitiveness of invasive weeds, and sedges share many of these traits with other plants (Table 1). The number of weeds reported in crops and nonagricultural areas is increasing. Two decades ago the important weeds in cotton (*Gossypium* spp.) worldwide slightly exceeded 100 species (Holm et al., 1977; Cronk & Fuller, 1995). Because of changes in production and cultural practices (especially reduced-tillage production

Table 1. Characteristics of weeds. Adapted from Muenscher (1955), Baker (1965, 1974), Klingman et al. (1982), Radosevich and Holt (1984), Stuckey and Barkley (1993), Rejmanek (1996), and Westbrooks (1998).

Copious production of small seeds
Early maturation
Extended seed dormancy and discontinuous germination
Germination and survival in a wide range of environments
Long life of propagules in soil or during dispersal
Profuse vegetative reproduction and fragmentation
Rapid growth
Short juvenile period
Self-compatible or if cross-pollinated then by wind or unspecialized floral visitors
Survival and the ability to produce seed under adverse environmental conditions
Seed size similar to associated crops or native plants
Structural modifications (e.g., thorns, prickles, spines, urticating hairs) that cause injury and repel animals or herbivores
Structural modifications facilitating dispersal
High photosynthetic rate (C_4 photosynthesis)
Increased water-use efficiency (C_4 photosynthesis)
Production of toxic secondary compounds that deter herbivores
Production of phytotoxins to prohibit or suppress growth of other plants (allelopathy)
Ability to parasitize other plants
Accumulation of large food reserves in roots, rhizomes, or other plant structures
Alternate host for insect pests and pathogens of crops
Resistance to pathogens
Small inconspicuous flowers
Short- and long-range dispersal mechanisms
Tolerance of environmental and chemical extremes, including fire, herbicides, and soil disturbances

systems), chemical control methods, weed shifts, adaptations of populations, evolution of herbicide-resistant weeds, and use of transgenic herbicide-resistant crops, the total number of important weeds in worldwide cotton production may currently exceed 200 species, as demonstrated by the total number recorded in cotton alone within the U.S.A. (Bryson et al., 1999). Natural barriers and restricted migration routes have historically prevented many plants from dispersing over great distances. However, the current speed and ease of world transportation by humans and cargo have increased the rate and distance of dispersal of plants. Upon introduction, if a species becomes naturalized, it may remain near the point of introduction without becoming a pest. In the case of invasive weeds, the local population amplifies and disperses, expanding the range. Unfortunately, newly introduced weeds often are undetected until after their numbers and ranges increase greatly. The period of time between introduction and invasion is the "lag phase" (Radosivich & Holt, 1984), the duration of which depends on a number of factors, e.g., size of population, dynamics of reproduction, and detection. The lag phase may vary from a few to many years, and facilitation of a naturalized population must occur before it expands, which may be brought about by new pathways for dispersal, introduction of new pollinators or dispersal vectors, environmental change (e.g., disturbance), and local adaptation through natural selection (Cronk & Fuller, 1995). Heterosis resulting from hybridization with related species may also be a factor in facilitation (Carter, 1990; Daehler & Strong, 1997).

Economics

There is little doubt that weeds cause severe economic losses, but placing an exact value on their impact worldwide is difficult, especially in natural or nonagricultural areas. In the U.S.A., economic loss due to invasive species (plants, animals, and pathogens) was estimated to be more than $138 billion per year (Westbrooks, 2001). Economic losses result from interference or competition with crops and forests and the costs of pest-control chemicals, fuel, equipment, labor, cultural-control practices, and additional irrigation and fertilizer (Chandler et al., 1984; Chandler & Cooke, 1992). Additional costs to human and animal health (i.e., allergies and toxins) are more difficult to estimate, but weeds, including sedges, cause substantial indirect economic losses worldwide.

In the U.S.A., it is estimated that cotton yields are reduced 8.5% by *Cyperus* L. weeds (Byrd, 1995a), a loss of about $40.5 million annually. The two primary *Cyperus* weeds in cotton and other row crops are *C. esculentus* L. (yellow nutsedge) and *C. rotundus* L. (purple nutsedge). In Mississippi alone, 31.4% and 23.5% of cotton fields are infested with *C. esculentus* and *C. rotundus*, respectively; however, population levels of *C. rotundus* were greater (75.6 aerial shoots/m^2) than those of *C. esculentus* (21.8 aerial shoots/m^2) (Byrd, 1995b). It is more difficult to estimate economic impact on nonagricultural areas, especially natural and public-use areas where losses are measured as reduction in tourism and recreation. Placing monetary values on native flora and fauna and wildlife habitat displaced or degraded by invasive species or the loss of the aesthetic value of a natural area is subjective and problematic. Control of weeds for the preservation of biological diversity is labor intensive and expensive, requiring manual labor where chemical methods may jeopardize natural plant communities (Randall, 1996). Upon control or eradication of invasive weeds, additional expense is incurred to prevent recolonization and to reintroduce native or innocuous nonindigenous niche replacements.

The importance of an agricultural weed is not necessarily correlated with its abundance within a crop but may depend on herbicide- and cultural-control regimes, soil type, climatic conditions, number of viable propagules in the seedbank, or other factors (McWhorter & Bryson, 1992). Some weeds may be abundant and conspicuous in crops without interfering, e.g., winter annuals that germinate, emerge, flower, and set seeds early enough so growth and yield of summer crops are unaffected. High population levels of *Isolepis carinata* Hook. & Arn. ex Torr. often occur in reduced-tillage cotton and soybean (*Glycine max* (L.) Merr.) in the southeastern U.S.A. (Bryson & Hanks, 2001). Because *I. carinata* completes its life cycle and dies early in the growing season, it does not adversely affect crop growth and yield. In agriculture, weeds that are difficult to control, compete with crops for light, nutrients, water, and space (Radosevich & Holt, 1984), interfere with crop harvest efficiency, or reduce quality of seed and lint (McWhorter & Bryson, 1992; Bryson et al., 1999) are the most important. Holm et al. (1977, 1997) list the world's most important agricultural weeds. Lists of weeds maintained by organizations include the Weed Science Society of America's *Composite List of Weeds* (WSSA, 1989) and Bayer AG's *Important Crops of the World and Their Weeds* (Bayer AG, 1992). Bayer AG (1992) is a more comprehensive worldwide list and includes more than 5000 scientific names of crops and weeds, while the WSSA lists about 2000 weeds found exclusively in the U.S.A. and Canada. Since the second edition of Bayer AG (1992), rights to the five-digit "Bayer codes" for weeds have been sold to the European Plant Protection Organization.

The economic, ethnobotanical, and horticultural importance of the family Cyperaceae is well documented (Simpson & Inglis, 2001). Many sedges are used as foods, food additives, drinks, fibers, animal poisons, and in the manufacturing of items including paper, perfumes, medicines, mats, boats, clothing, shoes, ropes, and roofing (Kükenthal, 1935–1936; Zeven & Zhukovsky, 1975; Darby et al., 1977; Allan, 1978; Burkill, 1985; Negbi, 1992; Stephens, 1994; Bryson et al., 1998; Simpson & Inglis, 2001). Tubers, rhizomes, seed, and foliage of sedges are important wildlife and domesticated animal feeds or forage (Hermann, 1970; Miller & Miller, 1999; Abad et al., 2000). Cyperaceae are also utilized for erosion control, revegetation after natural disturbances, and to amend and improve soil fertility (Tachholm & Drar, 1950; Hermann, 1970; Burkill, 1985; Fagotto, 1987; Simpson & Inglis, 2001). Traits that make sedge species useful for erosion control and soil stabilization also make them weeds.

Control Methods

Control methods for weedy sedges are diverse. Cultural methods of hand removal, hoeing, and draft plowing are still used in much of the world to control weeds including sedges (Shear, 1985). Mechanical tillage, flame cultivation, mowing, chemical treatments (herbicides and fumigants), cover crops (e.g., sweet potato [*Ipomoea batatas* (L.) Lam.]), and shading with a crop or black plastic have proven to be effective in controlling many sedge weeds of turf, pasture, and vegetable and row crops (Patterson, 1982; Glaze, 1987; Bryson & Keeley, 1992; Buchanan, 1992; Peterson & Harrison, 1995). As shown by Bryson et al. (2003a) with *Cyperus entrerianus* Boeckeler, mowing alone will not effectively control certain perennial sedge weeds, but it can prevent seed production if mowing intervals are shorter than the time required to set fertile achenes. Fumigants are usually applied on small areas to sterilize the soil for vegetable crop production. Herbicide treatments may vary depending on the susceptability of target species, crop tolerance, and required timing of application (McWhorter & Bryson, 1992). With each herbicide developed, research is conducted to determine the efficacy on weeds and the selectivity on crops (Holt et al., 1962; Hauser, 1963a, b; Duble et al., 1968, 1970; Hamilton, 1971; Hardcastle & Wilkinson, 1971; Keeley & Thullen, 1971; Keeley et al., 1972; Wills, 1972; Zandstra et al., 1974; Zandstra & Nishimoto, 1977; Wills & McWhorter, 1988; Grichar et al., 1992; Richburg et al., 1993, 1994; Wilcut et al., 1994; Vencill et al., 1995; Bryson et al., 2003b).

Effective methods of herbicide application include pre-emergence broadcast and incorporated (with tillage) applications to control unwanted sedges that germinate from seed, rhizomes, and tubers. Acceptable post-emergence treatments are dependent on the herbicide selectivity. Nonselective herbicides are applied in areas where nontarget species are of little concern, while selective herbicides are applied to control target sedges without harming crops or other desirable plants. Application technologies have been developed to spray or wipe nonselective herbicides on target weeds with special equipment (e.g., directed sprayers, hooded sprayers, recirculating sprayers, foam applicators, shielded sprayers, chemigation, control droplet applicators, air-assist systems, pneumonic applicators, sensing devices, electrically charged sprayers, and rope-wick applicators) to reduce or eliminate damage to crops (Burr & Warren, 1971, 1972; Wiese, 1986; Bryson & Wills, 1991; Wills et al., 1991; Barrentine et al., 1992; Bryson et al., 1992b, 1994a; Bryson & Hanks, 1993; Bryson, 1994, 1997). Directed sprayers and hooded sprayers are widely used in the U.S.A. for controlling *Cyperus rotundus*, *C. esculentus*, *C. iria* L. (rice flatsedge), and other weeds in cotton and soybean. Additives such as soaps and lightweight paraffinic oils effectively enhance activity of some herbicides (McWhorter, 1982; Bryson et al., 1990; Jordan, 1996). The development of herbicide-resistant, transgenic crops allows application of herbicides such as glyphosate over-the-top without damaging crops (Shaner & Lyon, 1980), while effectively controlling weeds. However, selection for herbicide-resistant sedges is a potential problem with the persistent use of a single herbicide or herbicide family (Dowler et al., 1974). Resistance to bensulfuron in *C. difformis* L. (smallflower umbrella sedge) populations is well documented in rice production (Pappas-Fader et al., 1993, 1994; Hill et al., 1994), and herbicide resistance is also known in other species (LeBaron, 1991).

Various pesticides also kill herbivores, predators, or pathogens of weeds, thereby potentially rendering weeds more competitive. For example, when nematocides control nematodes harmful to rice (*Oryza sativa* L.), they also kill nematodes attacking weeds of rice (e.g., *Echinochloa* spp. and *Cyperus haspan* L.) (Hollis, 1972).

Although several potential biological control agents (insects and pathogens) have been evaluated for controlling *Cyperus esculentus*, *C. rotundus*, and other sedges, none has been effective in reducing sedge populations outside controlled experiments (Phatak et al., 1987). It is unlikely that any single biological agent will provide total control of nutsedges (Morales-Payan et al., 2005). High parasitism and predation by other insects and use of pesticides that kill biocontrol agents are major constraints preventing effective biological control of sedges using insects in row crops (Frick, 1978). Excessive development, production, and registration costs, short shelf life, and ineffective delivery systems are major obstacles to utilizing pathogens

for biological control of weeds (Boyette, 2000; Duke & Boyette, 2001).

Population Dynamics

Weed species and population levels differ depending on land use, cropland preparation, forestation, and disturbance in natural areas. In agricultural systems, weed shifts occur primarily when management practices or environmental conditions change (McWhorter & Bryson, 1992; Murray et al., 1992). A single natural occurrence (e.g., tornado, hurricane, earthquake, fire, flood) or cultural- and chemical-control practices in farming operations may eliminate or reduce populations of one weed, while enhancing the survival, growth, and reproductive potential of another. As an example, farmers in the southeastern U.S.A. claimed that *Sida spinosa* L. seed and some sedge weeds such as *Cyperus esculentus* and *C. rotundus* arrived in containers of dinitroanaline (DNA) herbicides. In actuality however, DNA herbicides controlled annual grasses and small seed broadleaf weeds and vacated a niche for other weeds to invade areas previously not infested (Frans, 1969; Dowler et al., 1974). Weed shifts may also occur when environmental factors are modified through row spacing, irrigation, and crop rotation in row crops or when irrigation and fertilization frequency is increased on lawns, turf, and flowerbeds. In row crops, many sedge weeds thrive on irrigated soils and occur in higher population levels prior to crop canopy closure. Canopy closure earlier in the growing season shades weeds and prevents seed or tuber germination; thus, it is an effective cultural practice in controlling many weeds, including sedges such as *C. esculentus* and *C. rotundus* (Bryson et al., 1990, 2003b).

Weed shifts may also occur as weeds disperse into new areas. Non-native weeds, such as *Cyperus rotundus*, *C. iria*, *C. difformis*, and *Kyllinga brevifolia* Rottb., are excellent examples of weeds that were introduced into the U.S.A. more than a century ago and spread (Appendix 1). Within the past 50 years, sedge weeds such as *C. entrerianus*, *C. sanguinolentus* Vahl, and *C. eragrostis* Lam. have become established and spread rapidly in areas previously not infested in the U.S.A. (Carter, 1990, 2005; Carter & Bryson, 1996, 2000b; Bryson et al., 1998). Once introduced into a new area, weeds may take several years to become established before causing problems (the lag phase). Duration of the lag phase may vary depending on factors such as the number of seeds produced, presence of dispersal vectors, and environmental conditions (Radosevich & Holt, 1984). Early detection and implementation of control strategies are important in effectively controlling non-native invasive weeds soon after introduction or while still in the lag phase.

Farmers, consultants, and landowners must be ever observant of new weeds and changes within populations of weeds. Weed shifts are inevitable when land use is altered or disturbance occurs. For instance, weed shifts occur in reduced-tillage production systems or where cover crops are utilized (Bryson & Hanks, 2001). Perennial sedges such as *Cyperus esculentus* and *C. rotundus* and many other perennial weeds regenerate from greater soil depths than most annual weeds (Elmore, 1984; Elmore et al., 1989). Likewise, seeds of many annual sedges germinate on the soil surface following a rainfall event without burial, e.g., *C. sanguinolentus* (Carter & Bryson, 2000b). No-tillage or conservation crop production systems tend to favor weeds that germinate from shallow soil depths and perennial weeds. Unless controlled, perennial weeds are an increased problem in reduced-tillage production systems. Difficult-to-control perennial sedges such as *C. esculentus*, *C. rotundus*, and perennial *Kyllinga* Rottb. species often require repetitive and integrated control methods (Bryson & Keeley, 1992; McWhorter & Bryson, 1992; Bryson et al., 1999, 2003b).

In order to assess the impact of a particular weed species effectively, researchers have devised a method to determine the competitive potential of weeds based on field interference studies in agricultural and forest areas (Coble & Byrd, 1992; Reichard & Hamilton, 1997). Interference is ranked among weed species to develop a competitive index or relative competitive abilities table such as the one for selected weeds in cotton created by Coble and Byrd (1992). Such an index aids farmers, consultants, and landowners in determining which species are the most pernicious and helps establish thresholds for the number of weeds that can be tolerated in a given situation. Computerized models (e.g., Soybean Weed Control [SWC] and Mississippi State University Herbicide Application Decision Support System [MSUHADSS]) have been developed to aid farmers

and consultants in making recommendations, which take into account the weed-competitive index, herbicide options and prices, application costs, crop variety (cultivar), row spacing, crop stage, expected weed-free yield potential, expected selling price, soil moisture, and species of weed, population size, and density (Bryson, 2003). However, little research has been conducted to evaluate the thresholds of weeds in natural areas, where populations may far exceed threshold levels before a problem is perceived.

Identification

Accurate identification is essential in detecting the presence of weeds and developing the best management strategies for control (Palm et al., 1968; Murray et al., 1992). Traditionally, weed scientists have approached plant identification pragmatically and have adopted simplified systems to be used primarily by individuals with minimal training in systematic botany (e.g., Fischer et al., 1978; Stuckey et al., 1980; Elmore & Bryson, 1986–2001; DeFelice & Bryson, 2004). Such weed identification systems, usually very different from the dichotomous keys commonly used in taxonomic treatments, group weeds by similar susceptibility or resistance to herbicides, effectiveness of cultural-control practices, time of germination, and other factors (Bryson, 2003). In the simplest systems, plants are grouped into general categories (e.g., broadleaved species, grasses, sedges, annuals, or perennials), which is usually sufficient for making decisions about application of broad spectrum and nonselective herbicides. However, the increasing use of more selective herbicides and biological control agents demands greater precision in identification, i.e., determination to specific or infraspecific rank. Among sedges, susceptibility to herbicides is usually correlated with species; however, infraspecific biotypes (e.g., *Cyperus difformis*) do rarely exhibit differential resistance to herbicides (Pappas-Fader et al., 1993, 1994; Hill et al., 1994). In the case of herbicide-resistant biotypes, visual identification is impossible, necessitating the use of bioassays (LeBaron, 1991). Currently, when herbicide resistance is suspected, bioassays are used to determine if the lack of control is due to herbicide resistance, herbicide tolerance, environmental conditions, or misapplication.

Weed scientists and researchers in agriculture usually work with a relatively small subset of all possible plant species in their area, and the agricultural weeds are usually well known. Thus, simplified systems for identification generally work well for most common agricultural weeds. However, when new or unexpected weeds are encountered, more traditional taxonomic methods must be adopted (e.g., use of floristic manuals or systematic treatments in primary literature). Although it may be possible to identify immature sterile specimens of well-known sedges like *Cyperus esculentus* and *C. rotundus*, reliable identification of most sedges to species requires mature fertile specimens and oftentimes the assistance of taxonomic experts. To ensure that the specimen receives proper attention from a taxonomist, it should be prepared using standard methods and should include accurate geographical data (Carter, 2003). To avoid overlooking newly introduced weeds, every effort should be made to collect unfamiliar sedges and to identify them accurately. If one is not able to make a reliable identification, then the specimen with data should be sent to a competent taxonomist for determination. Vigilance, prompt action, and cooperation between plant systematists and weed scientists are absolutely essential in detecting newly introduced sedges and dealing effectively with emerging weed problems. Early detection and rapid response with effective control methods are essential for eradication of non-native invasive weeds (Westbrooks, 1998).

Factors Determining Competitive Advantage

The general characteristics of weeds summarized in Table 1 are found to varying degrees in many groups of plants, including sedges. Although no single species exhibits all features, it is presumed that there is usually a direct relationship between the number of these characteristics and the degree of invasiveness of a weed (Radosevich & Holt, 1984; Bryson & Carter, 2004). Most sedges reproduce sexually through the production of large numbers of small achenes. Such small reproductive structures are well suited to both short- and long-distance dispersal. Because of their small size, the achenes of sedges are difficult to detect and are readily transported as contaminants of seeds of crop, lawn, and forage plants. *Cyperus difformis* and *C. iria* are

major agricultural pests, particularly of rice (Holm et al., 1977). They probably originated as weeds by invading rice paddies in Asia, where they were subject to similar selective pressures as rice. Annual habit, rapid growth, short generation time, high fecundity, and tolerance of submergence of roots have enabled *C. difformis* and *C. iria* to persist and disperse as weeds of rice. *Cyperus difformis* completes its life cycle in just four to six weeks and can go through several generations within a single season (Holm et al., 1977), and an individual plant can produce as many as 50,000 achenes (Jacometti, 1912). These and other sedges are thought to have become naturalized throughout rice-producing areas around the world via dissemination of their achenes as contaminants of rice seed (Bellue, 1932; Muenscher, 1955; Kral, 1971).

Obviously, certain characteristics listed in Table 1 are more important as determinants of invasiveness than others. Given the importance of dispersal during the phases of introduction and spread of invasive species (Cronk & Fuller, 1995), characteristics relating to fecundity and dispersal of seeds would be of major importance, as would those providing the ability to spread vegetatively. According to Holm et al. (1977), *Cyperus rotundus* is the most pestiferous plant in the world. It reproduces and disperses primarily from vegetative tubers, with many biotypes rarely producing viable seeds (Wills, 1987). *Cyperus esculentus*, also a major agricultural weed, shares similar reproductive characteristics. Vegetative structures such as stolons, rhizomes, and tubers are important in localized spreading of many perennial sedges and may even be transported long distances both naturally and artificially when fragmentation occurs. Subterranean rhizomes, tubers, and corms also enable perennation and survival of sedges during adverse environmental conditions, e.g., cold temperatures, drought, or fire. Further discussion of dispersal in Cyperaceae, including dissemination of vegetative fragments and structural modifications facilitating transport of achenes and other structures, is included below in the Dispersal section.

The highly reduced and inconspicuous flowers of most sedges generally go undetected until after they produce seeds, which Muenscher (1955) cited as characteristic of many weeds. Cyperaceae are almost exclusively wind-pollinated (anemophilous). However, entomophily (insect pollination) has been documented to varying degrees in *Hypolytrum* Rich., *Mapania* Aubl., *Ascolepis* Nees ex Steud., *Rhynchospora* Vahl sect. *Dichromena* (Michx.) Griseb., *Cymophyllus* Mack., and even some species of *Bolboschoenus* (Asch.) Palla, *Carex* L., *Cyperus*, and *Eleocharis* R. Br. (Thomas, 1984a, b; Goetghebeur, 1998). Although there is a paucity of information, it is suspected that most sedges are cross-pollinated (allogamous). For example, *Cyperus esculentus* is self-incompatible, and therefore an obligate outcrosser (Brown & Marshall, 1981) with greater genetic variability within sexually reproducing populations than *C. rotundus*, which rarely produces viable seed (Horak & Holt, 1986; Horak et al., 1987). Cross-pollination in combination with anemophily is thought to contribute to the success of weeds (Baker, 1965, 1974). Some of the most pestiferous sedges are very broadly ranging, exhibiting great infraspecific diversity with many biotypes adapted to a wide variety of environmental conditions. *Cyperus rotundus* and *C. esculentus* are cosmopolitan weeds distributed widely throughout the tropics and throughout much of the temperate zone (Kükenthal, 1935–1936). In a worldwide treatment, Kükenthal (1935–1936) recognized numerous infraspecific taxa within these species, indicating considerable adaptation to local environmental conditions.

C_4 photosynthesis confers a competitive advantage under conditions of high temperature, high light intensity, and water stress (Hopkins & Hüner, 2004). C_4 plants have a lower transpiration ratio, thus, a higher water-use efficiency, than C_3 species, brought about by a lower CO_2 compensation point, reduced photorespiration, and enzymes (ribulose-1,5-bisphosphate carboxylase [RUBISCO], phosphoenolpyruvate carboxylase [PEPcase]) with higher optimal temperatures (Hopkins & Hüner, 2004). In Cyperaceae, C_4 photosynthesis is complex, consisting of four different anatomical types (chlorocyperoid, rhynchosporoid, fimbristyloid, eleocharoid) and two distinct carbon assimilation modes (Brown, 1975; Soros & Bruhl, 2000). In cladistic analyses using developmental, anatomical, and molecular data, Soros and Bruhl (2000) concluded that C_4 photosynthesis arose multiple times (at least four) in the Cyperaceae. Table 2 shows the occurrence of C_4 photosynthesis in the genera of cyperaceous weeds. In most cases genera are either C_3 or C_4; however, five genera, *Abildgaardia* Vahl, *Cyperus*, *Eleocharis*,

Table 2. The occurrence of C_3 and C_4 photosynthesis by genus of cyperaceous weeds.[1, 2, 3]

Mapanioideae (13/140)
- Hypolytreae (9/130)
  - *Mapania* (70) **C_3**
  - *Scirpodendron* (2) **C_3**
- Chrysitricheae (4/13)
  - *Lepironia* (1) **C_3**

Cyperoideae (71/2380)
- Scirpeae (6/60)
  - *Scirpus* (20) **C_3**
- Fuireneae (5/90)
  - *Fuirena* (30) **C_3**
  - *Bolboschoenus* (11) **C_3**
  - *Schoenoplectus* (50) **C_3**
  - *Actinoscirpus* (1) **C_3**
- Eleocharideae (3/200)
  - *Eleocharis* (200) **$C_3[C_4]$**
- Abildgaardieae (6/420)
  - *Abildgaardia* (10) **$C_4[C_3]$**
  - *Fimbristylis* (300) **$C_4[C_3]$**
  - *Bulbostylis* (100) **C_4**
- Cypereae (19/900)
  - *Cyperus* (incl. *Anosporum*, *Juncellus*, *Mariscus*, *Torulinium*) (550) **$C_4[C_3]$**
  - *Kyllinga* (60) **C_4**
  - *Queenslandiella* (1) **C_4**
  - *Pycreus* (100) **C_4**
  - *Lipocarpha* (35) **C_4**
  - *Oxycaryum* (1) **C_3**
  - *Isolepis* (60) **C_3**
  - *Courtoisina* (2) **C_3**
- Schoeneae (29/700)
  - *Rhynchospora* (250) **$C_3[C_4]$**
  - *Cladium* (4) **C_3**
  - *Lepidosperma* (55) **C_3**

Sclerioideae (15/340)
- Sclerieae (1/250)
  - *Scleria* (250) **C_3**

Caricoideae (5/2150)
- Cariceae (5/2150)
  - *Carex* (2000) **C_3**

[1] Data on photosynthetic pathway from Bruhl (1993,1995) and Soros and Bruhl (2000); $C_3[C_4]$ = mostly C_3, $C_4[C_3]$ = mostly C_4.

[2] Subfamily and tribal classification and numbers of genera and species in parentheses are from Goetghebeur (1998).

[3] Authority names for genera in Table 2 not discussed elsewhere in this paper are as follows: *Actinoscirpus* (Ohwi) R. W. Haines & Lye; *Cyperus* sect. *Anosporum* (Nees) Pax.

Fimbristylis Vahl, and *Rhynchospora* have both C_3 and C_4 species. Of these, the mostly aquatic to subaquatic *Eleocharis* is almost entirely C_3, and all of the subgenera of *Cyperus* are C_4 except *Pycnostachys* C. B. Clarke [= *Protocyperus*]. Although many weeds are not, some of the most competitive are characterized by C_4 photosynthesis (Black et al., 1969; Elmore & Paul, 1983). Holm et al. (1977) rank *C. rotundus*, *C. esculentus*, *C. difformis*, and *C. iria* among the world's worst weeds. *Cyperus rotundus*, *C. esculentus*, and *C. iria* are C_4 plants; *C. difformis* is C_3 (Hesla et al., 1982). Because C_4 photosynthesis is only one of many factors contributing to the competitiveness of weeds (Baskin & Baskin, 1978), it is not surprising that other characteristics enable certain C_3 Cyperaceae to be highly competitive weeds. C_4 photosynthesis is normally most advantageous in the terrestrial environment under conditions of drought, high light, and high temperatures (Hopkins & Hüner, 2004). *Cyperus difformis* is almost exclusively a pest of rice and is well adapted to aquatic environments, where excessive water in the environment ameliorates high temperatures, and water stress is normally not a factor. Thus, it is not surprising that *C. difformis* has C_3 photosynthesis. Similarly, the C_3 species *C. haspan* is a major weed of rice agriculture.

Although data on photosynthetic pathways for most species of cyperaceous weeds are lacking, generic-level data for species listed in Appendix 2 indicate a predominance of weeds in genera that are exclusively or primarily C_4 (Fig. 1). Thus, it appears that C_4 photosynthesis has been a major factor in the success of genera such as *Cyperus*, *Fimbristylis*, *Kyllinga*, and *Bulbostylis* DC. as weeds.

Certain plants, including weeds, achieve a competitive advantage through allelopathy, the production of chemical compounds that suppresses seed germination and growth in competing plants. Allelopathy is

well known in *Cyperus rotundus* and *C. esculentus* and has been cited as a factor in its competition with cotton and other crops (Friedman & Horowitz, 1971; Mallik & Tesfai, 1988; Martinez-Diaz, 1997). Although it has not been investigated, the nearly monotypic nature of invasive populations of *C. entrerianus*, observed in southern Louisiana and eastern Texas, U.S.A. (Carter, 1990; Carter & Bryson, 1996), suggests an allelopathic effect.

Weeds may also harbor insects and pathogens that adversely affect agricultural crops and native plants (USDA, 1960; Tietz, 1972). *Cyperus dives* Delile, the natural host for a moth (*Eldana saccharina* Walker) whose larvae cause losses to the sugar industry, is of some concern as a weed in southern Africa, where it is native and where an increase in its frequency is associated with clearing of natural vegetation for the cultivation of sugarcane (Gordon-Gray, 1995). *Cyperus papyrus* L. is also thought to harbor this same moth (Gordon-Gray, 1995). Noctuiid moth larvae of *Spodoptera frugiperda* (J. E. Smith) [= *Laphygma frugierda* (Abbott & Smith)] reportedly feed on *C. rotundus*, *Carex* spp., barley (*Hordeum vulgare* L.), cotton, milo (*Sorghum bicolor* (L.) Moench.), potato (*Solanum tuberosum* L.), rice, soybean, sweet potato, and other crops and native plant species (Tietz, 1972). *Colletotrichum graminicola* (Ces.) G. W. Wils., a fungal pathogen, infects *Carex* spp., other Cyperaceae, and grass crops (USDA, 1960). *Cyperus esculentus*, *C. rotundus*, chili peppers (*Capsicum annuum* L.), and other crops are hosts to the southern root-knot nematode (*Meloidogyne incognita* (Kofoid & White) Chitwood) (Schroeder et al., 1993).

Dispersal

Dispersal is fundamentally important in determining distributional patterns of plant species. Dispersal may be complex and dynamic involving both sexual and asexual systems, multiple vectors, and shifts in vectors. When released from competition, predation, and disease, many species, upon introduction outside their natural ranges, have potential to become weeds. Dispersal is crucial at two points during invasion by plants: first, during the initial introduction of the species and later, after naturalization, as the invasive species spreads, expanding its range (Cronk & Fuller, 1995). Consequently, basic knowledge about attributes of reproduction and natural dispersal can provide insight into which species are likely to become invasive weeds and how they might be dispersed.

Vegetative growth from rhizomes, stolons, runners, tubers, and corms is common in many perennial sedges and is undoubtedly very important in local expansion. Some species, e.g., *Eleocharis melanocarpa* Torr., *E. microcarpa* Torr., and *E. rostellata* Torr., have arching aerial stems that take root apically upon contact with the ground, and others, like *E. vivipara* Link, proliferate vegetatively from spikelets. *Cyperus pectinatus* Vahl forms plantlets vegetatively from its inflorescence (Haines & Lye, 1983). Vegetative growth when coupled with fragmentation and transport of asexual propagules can also result in more distant dispersal. This is perhaps most effective in the dispersal of fragments broken from rafts (sudds) of floating or submerged natant aquatic sedges by water currents or wind. Such dispersal has been noted in *C. cephalotes* Vahl, *C. colymbetes* Kotschy & Peyr., *C. mundtii* Kunth, *C. papyrus*, *C. pectinatus*, and *Oxycaryum cubense* (Poepp. & Kunth) Palla (Kern, 1974; Haines & Lye, 1983; Gordon-Gray, 1995). We have noted this phenomenon in *C. alopecuroides* Rottb., *C. prolifer* Lam., *Eleocharis baldwinii* (Torr.) Chapm., *E. vivipara*, and *O. cubense* and suspect that it occurs in other species similar in habit and habitat, e.g., *C. elatus* L. and *Websteria confervoides* (Poir.) S. S. Hooper (Kern, 1974).

Sedges exhibit a variety of modifications exploiting various agents of dispersal, most of which directly involve fruits or inflorescences. A number of mechanisms involving dispersal of achenes by wind (anemochory) are known in Cyperaceae. In *Afrotrilepis* (Gilly) J. Raynal, *Carpha* Banks & Sol. ex R. Br., *Costularia* C. B. Clarke, *Eriophorum* L., and *Scirpus* L., a persistent perianth adnate to the achene is modified into long, silky bristles or hairs that facilitate transport by wind (Kern, 1974; Pijl, 1982; Haines & Lye, 1983; Goetghebeur, 1998), and in *Androtrichum* Brongn. and *Machaerina* Vahl, persistent elongated filaments have the same function (Goetghebeur, 1998). Also, the flattened wing-like floral scales of *Anosporum* spp. and the flattened winged spikelets of certain *Kyllinga* spp. (Haines & Lye, 1983) promote wind dispersal of the achenes retained within. Such dispersal of spikelets has been

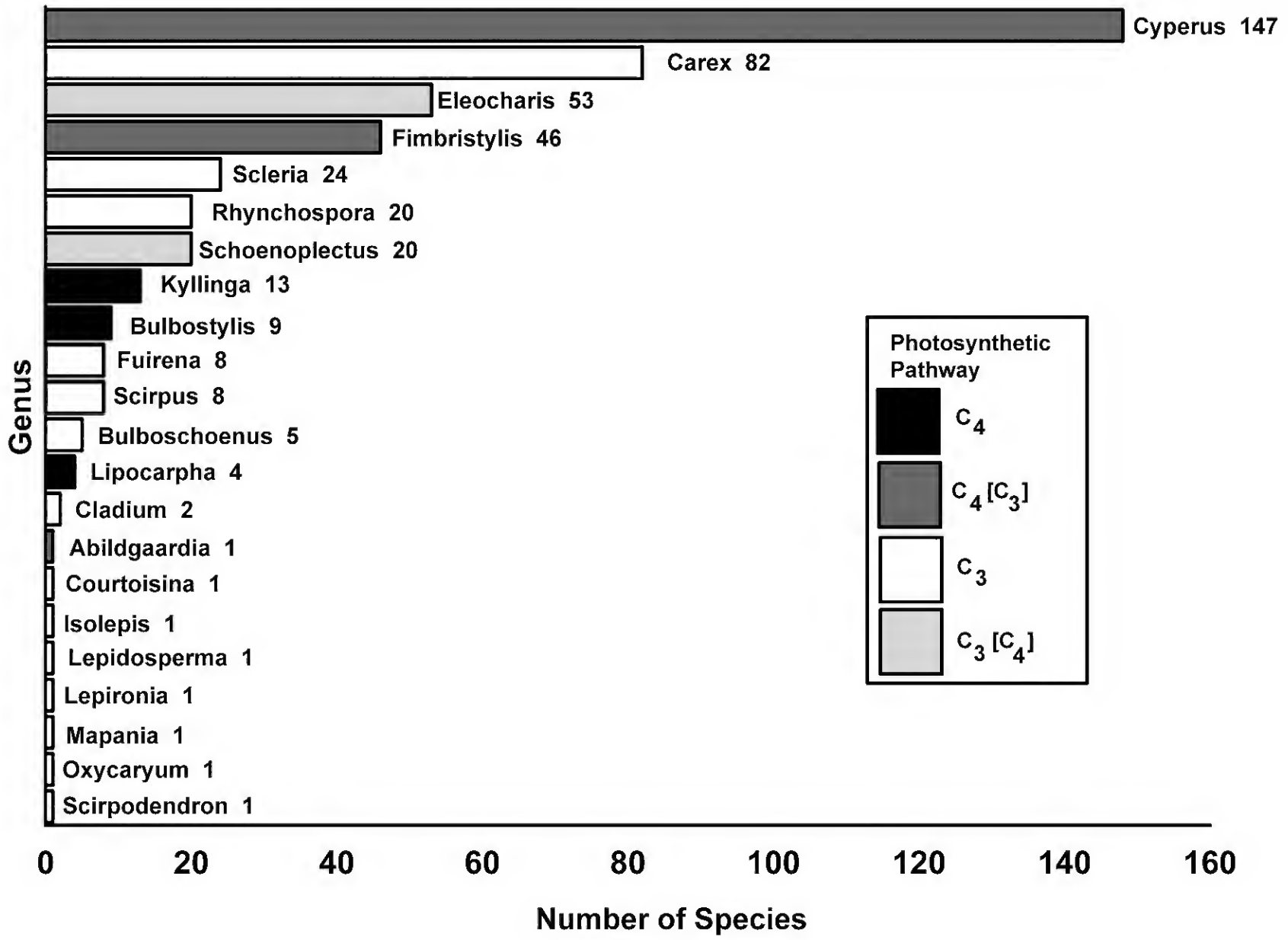

Figure 1. Photosynthetic pathways among genera of Cyperaceae with weeds; data on photosynthetic pathways from Bruhl (1993, 1995) and Soros and Bruhl (2000).

observed over short distances during collection of specimens of the introduced weed *K. squamulata* Thonn. ex Vahl (Carter, pers. obs.).

Dispersal by water (hydrochory) is well documented in Cyperaceae. The fruits or spikelets of most terrestrial sedges are disseminated to some extent by rain; however, such dispersal is usually quite local (Ridley, 1930). The achenes of the aquatic and wetland sedges *Cyperus (Anosporum) colymbetes*, *C. pectinatus*, *C. platystylis* R. Br., *Oxycaryum cubense*, several *Scirpus* spp., and certain wetland *Carex* spp. have a spongy suberized pericarp that facilitates flotation and dispersal by moving water (Chermezon, 1924; Ridley, 1930; Kern, 1974; Lye, 1981; Haines & Lye, 1983). Achenes of *Cladium* P. Browne were observed to float in the laboratory for up to 15 months (Ridley, 1930). Similarly in *Cyperus odoratus* L. and *Remirea maritima* Aubl., the achene remains enclasped in a buoyant corky rachilla and is thereby dispersed by moving water (Kern, 1974; Haines & Lye, 1983). Floods undoubtedly transport even unmodified, nonbuoyant achenes, vegetative fragments of plants (e.g., rhizomes, tubers), and whole plants (Kern, 1974) and deposit them far from the main channel along basins of major rivers. *Cyperus fuscus* L., a potential rice weed in the U.S.A., has apparently been dispersed by floodwaters along the Missouri River in the central U.S.A. (McKenzie et al., 1998).

Dispersal of achenes by animals (zoochory), especially birds, is important in Cyperaceae. Zoochory may involve the internal (endozoic) transport of achenes within the digestive system or external (epizoic) transport. The achenes of *Carex*, *Cladium*, *Cyperus*, *Fimbristylis*, *Rhynchospora*, and *Scirpus* have been identified in the alimentary systems of waterfowl (Ridley, 1930). Waterfowl and other birds consume large quantities of achenes,

especially of *Cyperus* spp. and *Eleocharis* spp., and their endozoic transport plays an important role in dispersal of sedges over long and short distances (Ridley, 1930; Kern, 1974; Haines & Lye, 1983). Vlaming and Proctor (1968) experimentally determined that sedge achenes remained viable after retention in avian digestive systems for periods up to 120 hours: *Cyperus ochraceus* Vahl, max. 37 hr.; *Eleocharis albida* Torr., max. 38 hr.; *E. macrostachya* Britton, max. 77 hr.; *E. parvula* (Roem. & Schult.) Link ex Bluff, Nees & Schauer max. 30 hr.; and *E. quadrangulata* (Michx.) Roem. & Schult., max. 120 hr. Brightly colored fruits in the tropical genus *Gahnia* J. R. Forst. & G. Forst. are consumed and dispersed by birds (Benl, 1937; Pijl, 1982; Lye, 2000), and, according to Sauer (1988), seeds of *Carex nigra* (L.) Reichard were brought to Iceland by snow buntings from Great Britain. Short-distance endozoic dispersal by cattle (*Carex*, *Scirpus*) and water buffalo (*Fimbristylis globulosa* (Retz.) Kunth, *F. littoralis* Gaudich.) has been reported by Kern (1974).

Similarly, the epizoic transport of achenes in mud adhering to the feet of migratory waterfowl is implicated in long-distance dispersal in *Cyperus*, *Eleocharis*, *Rhynchospora*, and *Scirpus* (Ridley, 1930; Kern, 1974). Such mechanisms could account in part for the wide distributions of *C. drummondii* Torr. & Hook., *C. odoratus*, *C. virens* Michx., and *Oxycaryum cubense*. A number of epizoic mechanisms involving various structural modifications are known in Cyperaceae. The achenes of many species of *Eleocharis*, *Fuirena* Rottb., *Rhynchospora*, *Schoenoplectus* (Rchb.) Palla, and *Websteria* S. H. Wright are subtended by persistent, hypogynous bristles beset with retrorse barbs that readily attach to feathers or hair of animals (Kern, 1974; Haines & Lye, 1983), and the North American sedge, *C. plukenetii* Fernald, exhibits a number of modifications that facilitate dispersal of intact spikelets by attachment to animal hair (Carter, 1993). *Uncinia* Pers., widely distributed in the Southern Hemisphere, including many islands of the Pacific, is characterized by a hooked inflorescence axis that extends beyond the utricle, attaching readily to feathers and enabling transport by birds (Pijl, 1982; Mabberley, 1997). *Carex pauciflora* Lightf. has a springing mechanism that disperses its perigynia over relatively short distances when touched by animals (Hutton, 1976), and the perigynia of certain other *Carex* spp. produce oil-rich appendages and are dispersed by ants (Handel, 1976, 1978; Gaddy, 1986). Similarly, a fleshy perianth in *Lepidosperma* Labill. reportedly facilitates dispersal by ants (Goetghebeur, 1998).

High fecundity and small fruits (achenes) make sedges especially susceptible to unintentional dissemination directly by humans or through their activities. A variety of human activities are known or suspected to disperse sedges, and most of these involve movement of their small, inconspicuous achenes. Sedge achenes are readily dispersed as contaminants of commercial seed supplies (Koyama, 1985; Bryson & Carter, 1992; Sell & Murrell, 1996), and achenes or even live plants may contaminate ornamental nursery stock, potted plants, or mulch. A number of sedges associated with rice agriculture around the world (cf. *Bolboschoenus*, *Cyperus*, *Eleocharis*, *Fimbristylis*, *Schoenoplectus* in Appendix 1) are thought to have dispersed via achenes as contaminants of rice seed (Bellue, 1932; Muenscher, 1955; Kral, 1971). Shipments of shorn wool may contain achenes of sedges, which when dispersed result in the introduction of so-called "wool aliens" (Sell & Murrell, 1996). Other kinds of cargo, including live animals, transported by land, sea, or air may harbor achenes resulting in the unintentional introduction of sedges (Carter & Mears, 2000). Dumping of ballast contaminated with achenes or vegetative propagules (e.g., rhizomes, stolons, tubers) has long been associated with dispersal of sedges and other plants (e.g., Smith, 1867; Brown, 1880; Britton, 1886; Mohr, 1901). The inadvertent transport of achenes or vegetative propagules embedded in mud or lubricants adhering to wheels or other parts of freight cars, trucks, automobiles, and airplanes undoubtedly disperses sedges, and migration of plants, including sedges, along railroads (ferroviatic migration) is well documented (e.g., Mühlenbach, 1979, 1983). It also seems likely that tiny achenes of sedges, drawn by jet airplane engines, could lodge in the housing of the engine or other parts and be carried great distances. The transport of turfgrass sod, mulch, soil, hay, and fodder has been associated with dispersal of sedges, e.g., *Cyperus esculentus*, *C. rotundus*, *Kyllinga brevifolia*, and *K. gracillima* Miq. (Bryson et al., 1992b, 1996, 1997; Sell & Murrell, 1996), and movement of achenes and vegetative propagules occurs during construction and maintenance of roads, e.g., *Cyperus entrerianus*, *C. sanguinolentus*, *Carex oklahomensis* Mack., and

C. praegracilis W. Boott (Kern, 1974; Reznicek & Catling, 1987; Carter, 1990; Carter & Bryson, 1996, 2000b).

Because sedges are generally inconspicuous, and other than as weeds are of minimal economic importance, they escape all but casual notice and interest of most humans; consequently, it is presumed that the intentional dispersal of sedges by humans is infrequent. However, as shown in Appendix 1 and in Figures 2 and 3, there is an increased interest in using sedges as ornamentals, and a surprising number of species are subject to deliberate transfer by humans. Some of these have become naturalized weeds from cultivation, and any could potentially become pests. *Carex comans* Berggr., *C. morrowii* Boott, *C. pendula* Huds., *C. riparia* Curtis, *Cymophyllus fraserianus* (Ker Gawl.) Kartesz & Gandhi, *Cyperus compressus* L., *C. eragrostis*, *C. longus* L., *C. owanii* Boeckeler, and *C. strigosus* L. are used in gardens, and *Carex baccans* Nees, *Cyperus albostriatus* Schrad., *C. fertilis* Boeckeler, and *Isolepis cernua* (Vahl) Roem. & Schult. are sometimes used as potted plants or in hanging baskets (Bailey, 1935, 1949; Bailey & Bailey, 1976; Everett, 1980–1982; Brickell & Zuk, 1997). Of these, *Carex riparia*, *Cyperus compressus*, *C. eragrostis*, and *C. longus* are listed as weeds (cf. Appendix 2), and the South African *C. owanii* is naturalized, but apparently not invasive, in California, U.S.A. (Tucker et al., 2002).

Cyperus alternifolius L. subsp. *flabelliformis* Kük. (umbrella plant, umbrella sedge) has been used as an ornamental in water gardens and as a potted plant for more than 200 years (Bailey & Bailey, 1976). It is widely naturalized from cultivation throughout the tropics and subtropics (Kern, 1974; Koyama, 1985) and is frequently cited as a weed (cf. Appendix 2). Other sedges cultivated in water gardens include *C. papyrus* (papyrus), *C. prolifer* (dwarf papyrus, miniature papyrus), *C. sexangularis* Nees, *C. textilis* Thunb., and various bulrushes, *Bolboschoenus robustus* (Pursh) Soják, *Schoenoplectus acutus* (Muhl. ex J. M. Bigelow) Á. Löve & D. Löve, *S. heterochaetus* (Chase) Soják, *S. tabernaemontani* (C. C. Gmel.) Palla, *S. lacustris* (L.) Palla, and *Scirpus cyperinus* (L.) Kunth (Bailey, 1935, 1949; Everett, 1980–1982; Gordon-Gray, 1995). *Cyperus papyrus* is naturalized in Australia (Wilson, 1993) and in Florida, U.S.A. (Wunderlin, 1998), and *C. prolifer* is naturalized in Florida (Carter et al., 1996).

Appendix 1 is a list of sedges known or suspected to be transported by human activities. The frequencies of various modes of anthropogenic dispersal in Cyperaceae are shown in Figure 2: ornamentals (53%); wool aliens (13%); ballast (7%); rice agriculture (7%); revegetation, reclamation, erosion control, and soil improvement (7%); and highways and railroads (3%). The burgeoning human population and the current ease and frequency of rapid long-distance transportation of humans and cargo make it inevitable that such dispersal of sedges, both unintentional and deliberate, will continue into the foreseeable future.

Invasion by *Cyperus entrerianus*: A Case Study

The following case study of *Cyperus entrerianus* (deeprooted sedge), based upon Carter (1990) and subsequent investigation (Carter, unpubl. data), shows how basic research in the field and the herbarium allows for the detection of invasive weeds and illustrates the need for accurate and timely identification in order to take appropriate action against them. In 1987, Carter found a species of *Cyperus* in Ware County, Georgia, that did not fit any descriptions of species known from the southeastern U.S.A. During 1988 and 1989, intensive searching in the field resulted in discovery of numerous additional populations of this perplexing sedge in Florida, Georgia, Alabama, Louisiana, and eastern Texas. During this same period, an examination of herbarium specimens at FSU, IBE, and VDB revealed additional ones, variously misidentified, that were collected from northern Florida in the 1970s and 1980s, southern Louisiana in 1975, and eastern Texas in 1981. In early 1989, Carter correctly determined that the enigmatic sedge was *C. entrerianus*.

Based upon data gleaned from herbarium specimens and intensive field research and Rosen et al. (2006), the following hypothetical scenario for the introduction, naturalization, and dispersal of *Cyperus entrerianus* in the U.S.A. is proposed (Fig. 4). *Cyperus entrerianus* was introduced into the U.S.A. before 1941, and the suspected points of introduction are Cameron County, Texas, and Pensacola, Florida (*Brinker 413*, US). The species was not found again in

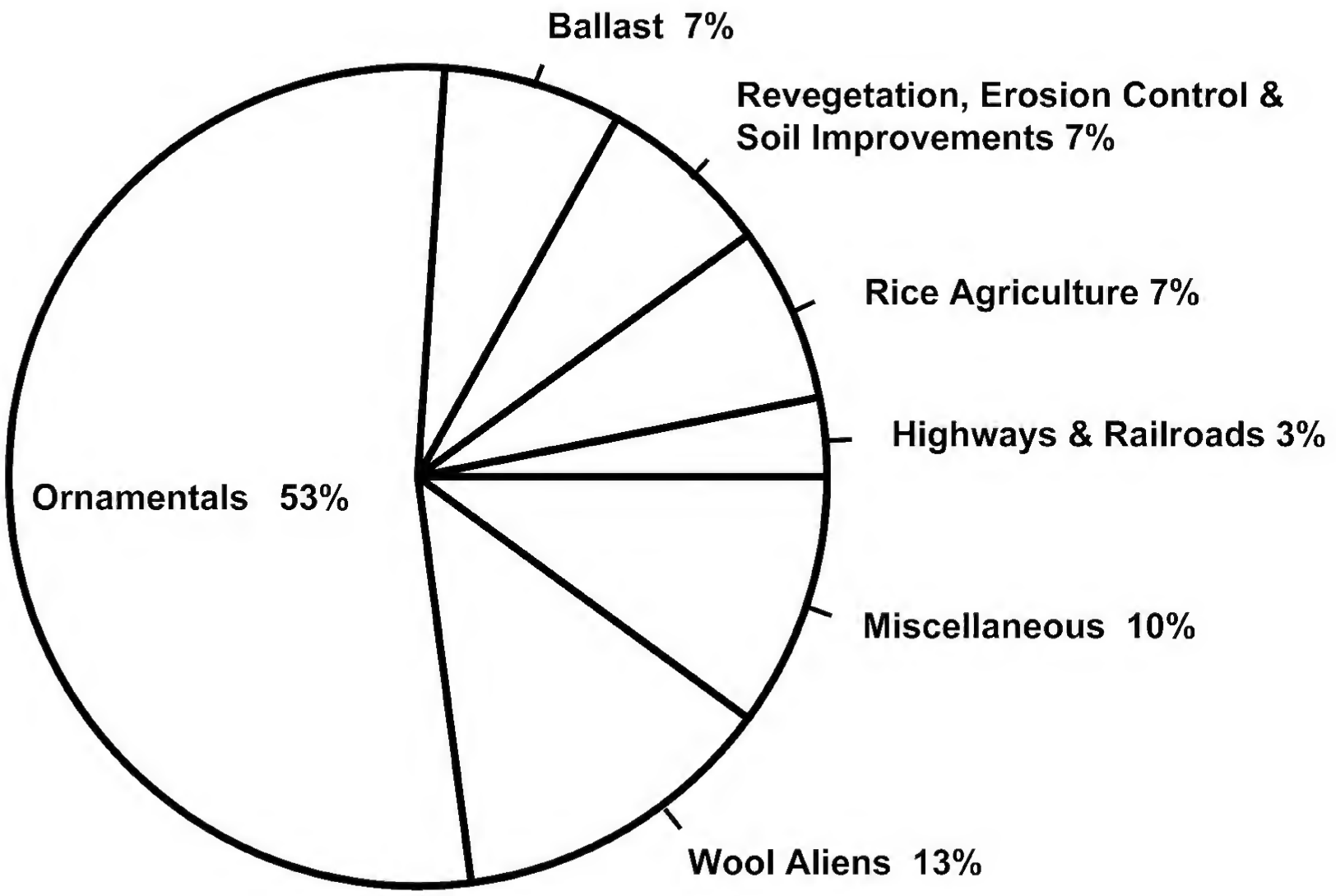

Figure 2. Percentages of various kinds of anthropogenic dispersal of cyperaceous weeds listed in Appendix 1.

the U.S.A. until 1974, when it was collected again in Pensacola (*Godfrey 73755*, FSU). It was collected in southern Louisiana in 1975 (*Allen 6674*, VDB), additional collections were made in Escambia and Gulf counties, Florida, during the late 1970s and 1980s, and it was found in eastern Texas in 1981 (Carter, 1990). All of the collections of *C. entrerianus* made by others before it was reported new to the U.S.A. by Carter (1990) were variously misidentified as *C. pseudovegetus* Steud., *C. robustus* Kunth, *C. virens*, and *C. virens* var. *drummondii* (Torr. & Hook.) Kük. The paucity of herbarium records before the mid-1980s suggests that *C. entrerianus* was in its lag phase until then. Although the apparent rapid expansion of range in the late 1980s and 1990s is undoubtedly in part an artifact of intensive searching for *C. entrerianus* by Carter and others (Carter, 1990; Carter & Jones, 1991; Bryson & Carter, 1994; Carter & Bryson, 1996), its collection at a number of sites in Louisiana and Florida during the later 1970s by researchers who had no knowledge of its correct identity indicates that its lag phase had ended some years earlier.

It is suspected that *Cyperus entrerianus* was introduced independently in southern Texas and at Pensacola from temperate South America or Mexico (Carter, 1990; Rosen et al., 2006). There are other cases of introduced *Cyperus* weeds that were probably imported into Pensacola via ballast: *C. aggregatus* (Willd.) Endl., *C. difformis*, *C. pilosus* Vahl, and *C. reflexus* Vahl (Burkhalter, 1985; Wunderlin, 1998); thus, introduction of *C. entrerianus* via ballast is plausible. Distribution and habitat indicate that *C. entrerianus* has spread from its point of introduction at Pensacola via dispersal from road construction and maintenance activities, primarily along highway Interstate 10 and secondarily along intersecting highways (Carter, 1990; Carter & Bryson, 1996). It is probably also now dispersed endozoically by birds or other animals that consume its achenes. Certain populations of *C. entrerianus* in the southeastern U.S.A. show evidence of introgression with *C. surinamensis* Rottb., which could account in part for the robust habit (heterosis) observed in plants there (Carter, 1990). Vigorous growth and robust form have probably facilitated the rapid expansion of *C. entrerianus* in the southeastern

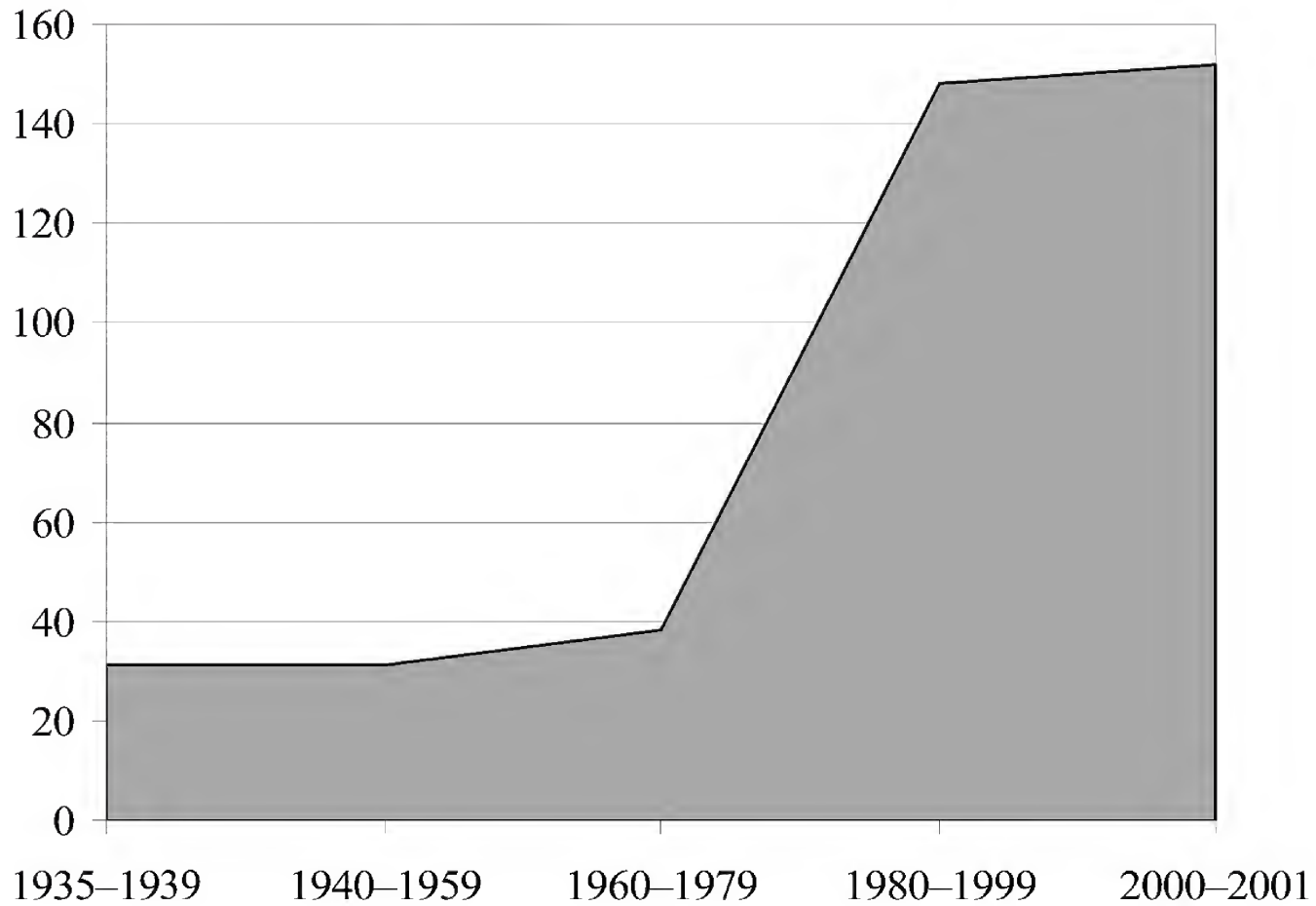

Figure 3. Cumulative numbers of ornamental and cultivated species of Cyperaceae listed in selected horticultural references from 1935 to 2001.

U.S.A. from Florida and southern Georgia west into eastern Texas, and it has begun to invade natural areas in eastern Texas (Rosen et al., 2006).

Survey of Genera and Selected Species

There is no comprehensive, contemporary, cosmopolitan enumeration and description of species of Cyperaceae, and such comprehensive accounts of most cyperaceous genera do not exist. Furthermore, there is still considerable disagreement about taxonomic limits and circumscriptions of many genera. Consequently, estimates of numbers of taxa (genera/species) vary considerably: ca. 70/ca. 4000 (Cronquist, 1981); 98/4350 (Mabberley, 1997); 104 genera/5000+ (Goetghebeur, 1998); ca. 100/ca. 5000 (Ball et al., 2002). For example, there is little consensus about the circumscription of *Cyperus*, i.e., whether it should be defined broadly to include *Diclidium* Schrad. ex Nees, *Juncellus* C. B. Clarke, *Kyllinga*, *Mariscus* Vahl, *Pycreus* P. Beauv., and *Queenslandiella* Domin with infrageneric rank, or whether it should be defined narrowly with the segregates treated as genera. This problem has major implications with respect to nomenclature in *Cyperus*, the most important genus of weeds in the family (Carter & Bryson, 2000a). Use of molecular techniques (e.g., Muasya et al., 2000a, b) should help to stabilize nomenclature by resolving the taxonomic status and rank. However, until such basic problems are resolved through additional research and alignment of nomenclature, we think a conservative approach is warranted. Herein where possible, nomenclature at the generic level follows the recently published *Flora of North America*, volume 23. However, in the absence of a synonym under *Cyperus*, one species, *Pycreus decumbens* T. Koyama, reported as a weed in Brazil by Kissmann (1997), was not listed in Appendix 2. *Cyperus decumbens* Govind., the name for a different species from India published in 1973, prevents legitimate transfer of the name under *Cyperus*.

Based upon a survey of more than 60 publications, Appendix 2 is a worldwide list that includes 449 species of Cyperaceae that have been cited as weeds. Additionally, we have included other sedges indigenous to the southeastern U.S.A. that we have observed to be weeds. Table 3 summarizes numbers of weedy species by genus. *Cyperus* is by far the

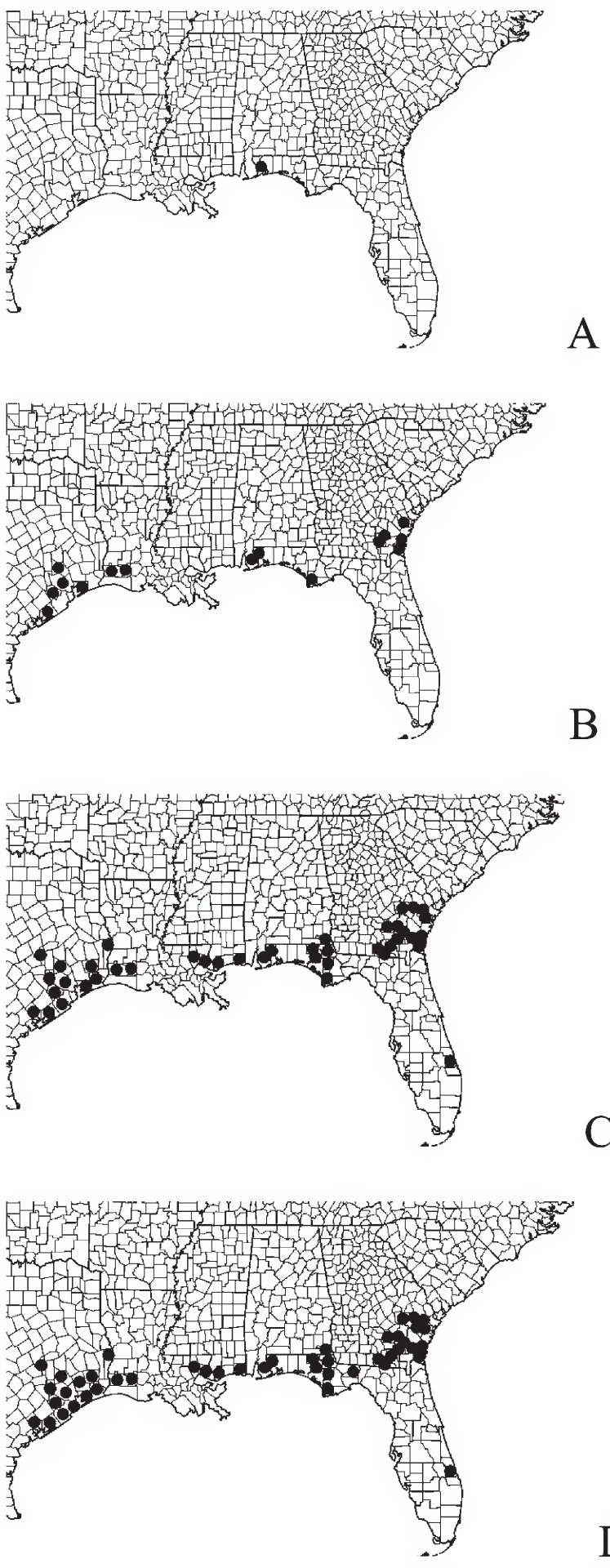

Figure 4. The dispersal of *Cyperus entrerianus* Boeckeler in the U.S.A. —A. 1941–1979. —B. 1941–1989. —C. 1941–1999. —D. 1941–2003.

largest genus with more than 147 species or 33% of the total, followed by *Carex* with 82 species and 18%, *Eleocharis* with 53 species and 12%, *Fimbristylis* with 46 species and 10%, and *Scleria* P. J. Bergius with 24 species and 5%. *Schoenoplectus*, *Rhynchospora*, *Kyllinga*, *Bulbostylis*, *Fuirena*, *Scirpus*, and *Bolboschoenus* had fewer than 5% each, and the remaining 10 genera had fewer than 1% each. Cypereae, which includes *Cyperus*, is the largest tribe of weeds (Fig. 5), and subfamily Cyperoideae, which includes Cypereae, has the overwhelming majority of weedy sedges (Fig. 6).

The previous lists of Holm et al. (1977, 1979, 1997) and WSSA (1989) show a substantially larger proportion of weeds in *Cyperus* (ca. 42%); ca. 43% in *Eleocharis*, *Fimbristylis*, *Scirpus* (incl. *Bolboschoenus*, *Isolepis* R. Br., *Schoenoplectus*); and the remaining 15% in *Carex*, *Cladium*, *Fuirena*, *Kyllinga*, *Rhynchospora* (incl. *Dichromena*, *Psilocarya* Torr.), and *Scleria*. Our survey (Appendix 2) shows a much smaller proportion in *Cyperus* and substantial increases in *Carex* and other genera. Bayer AG (1992) was not used in compiling Appendix 2 because it does not separate weeds from crops and because it is based upon key sources cited in Appendix 2.

ABILDGAARDIA

Abildgaardia is a genus of ca. 15 species distributed mostly in the pantropics and subtropics in both the Eastern and Western hemispheres (Kral, 2002d). Although *Abildgaardia* spp. have been placed in *Bulbostylis* and *Fimbristylis*, embryological and anatomical data support segregation as a separate genus (Lye, 1973). The results of our survey (Appendix 2) show only one species, *A. ovata* (Burm. f.) Kral, cited as a weed, which is reported to be a weed in Asia, North America, and the Pacific Islands (Holm et al., 1979). In southern Florida, U.S.A., it is occasionally a weed of gravelly soils in waste areas, along highways, and in lawns (Carter, pers. obs.).

BOLBOSCHOENUS

Bolboschoenus is a genus of 6 to 15 species (Smith, 2002a), five of which are listed as weeds in Appendix 2. *Bolboschoenus maritimus* (L.) Palla, considered among the world's worst weeds, is a pest in agricultural lands and waterways in Africa, Asia, Australia, Europe, and North and South America (Holm et al., 1997; Kissmann, 1997). It is a troublesome rice weed in paddy fields (Holm et al., 1977, 1997), and in the southern Korean peninsula *B. maritimus* infests more than 80% of rice fields reducing yields by as much as 50% when adequate control

Table 3. Numbers and percentages of cyperaceous weeds by genus (data extracted from Appendix 2).

Genus	Species (infrasp.)	Percent of Total
Cyperus[1]	147 (2)	33
Carex	82	18
Eleocharis	53	12
Fimbristylis	46	10
Scleria	24	5
Rhynchospora	20	4
Schoenoplectus	20	4
Kyllinga	13	3
Bulbostylis	9	2
Fuirena	8	2
Scirpus	8	2
Bolboschoenus	5	1
Lipocarpha	4	< 1
Cladium	2	< 1
Abildgaardia	1	< 1
Courtoisina	1	< 1
Isolepis	1	< 1
Lepidosperma	1	< 1
Lepironia	1	< 1
Mapania	1	< 1
Oxycaryum	1	< 1
Scirpodendron	1	< 1
Total	449 (2)	100

[1] Includes *Diclidium*, *Juncellus*, *Mariscus*, *Pycreus*, and *Queenslandiella*.

measures are not taken (Ryang et al., 1978). Integrated weed management schemes, including rotation of crops, water regimes, and chemical and cultural methods, effectively control *B. maritimus* in rice-producing areas of Asia (De Datta & Jereza, 1976; Verga et al., 1977). *Bolboschoenus maritimus* is less a problem in the equatorial zone than in semitropical and temperate regions of the world (Holm et al., 1997). The achenes of *B. maritimus* are readily dispersed by birds (Holm et al., 1997) and by water (Guppy, 1893). *Bolboschoenus fluviatilis* (Torr.) Soják is reported as an aquatic weed in Asia, Australia, and North America (Holm et al., 1979; WSSA, 1989).

BULBOSTYLIS

Bulbostylis is a genus of ca. 100 species, occurring mostly in dry or periodically dry, sunny, sandy uplands and savannas in warm temperate and tropical regions worldwide (Kral, 2002c). Nine species are listed as weeds in Appendix 2; however, none is a major weed. *Bulbostylis barbata* (Rottb.) C. B. Clarke and *B. capillaris* (L.) C. B. Clarke are occasionally weeds of sandy soil in flowerbeds and poorly managed turf in the southeastern U.S.A. In late summer and fall in the Coastal Plain of the southeastern U.S.A., *B. barbata* can be a conspicuous feature of the landscape when en masse its reddish brown inflorescences appear in sandy cultivated fields (Kral, 1971). *Bulbostylis capillaris* and *B. ciliatifolia* (Elliott) Fernald are common weeds of sandy fallow fields, roadsides, and on gravel and cinders of railroad right-of-ways (Kral, 1971; Godfrey & Wooten, 1979). All three species often grow in sandy soil in flowerbeds and lawns or through cracks in sidewalks and parking lots. *Bulbostylis barbata* is reported as a weed of cultivated lands in Taiwan (Lin, 1968), and *B. capillaris* is reported as a weed in Brazil (Kissmann, 1997).

CAREX

Of the more than 2000 species worldwide (Ball & Reznicek, 2002), only a small proportion of *Carex* spp. are major weeds when compared to other sedge groups (e.g., *Cyperus*, *Kyllinga*). Although not among the most troublesome weeds of rice, *Carex diandra* Schrank and *C. pycnostachya* Kar. & Kir. are reported from rice field habitats in Pakistan (Kukkonen, 2001). Very few *Carex* spp. are invasive, and none is a principal agricultural weed (Holm et al., 1977), which may be due to several factors including more restrictive habitat requirements, fewer or larger seeds, shorter period of sexual reproduction, fewer vectors for dispersal, lack of tolerance to mowing or tillage, and greater susceptibility to herbicides. In Appendix 2, 82 species of *Carex* are listed as weeds.

Carex blanda Dewey and *C. leavenworthii* Dewey are occasional weeds of poorly kept lawns, especially under shade of deciduous trees in the southeastern U.S.A. (Bryson, 1985a). *Carex blanda* is often locally abundant and capable of being weedy in diverse environmental and edaphic conditions (Bryson & Naczi, 2002). It is highly likely that *C. blanda* and other weedy *Carex* species are dispersed as contaminates of grass seed, sod, or clippings for turf establishment (Jones et al., 1993). In lawns and on golf courses, *C. blanda* and *C. leavenworthii* are controlled by frequent mowing and herbicide treatments (Bryson, 1985a). Listing of *C. cephalophora* Muhl. ex Willd. as a weed (Callahan et al., 1995) may be due to taxonomic confusion with *C. leavenworthii* and literature that considered the two taxa conspecific. Another occasional lawn weed, *C. cherokeensis* Schwein., is a weed of pastures (Burns & Buchanan, 1967; Burns et al., 1969; Bryson, 1985a). In the Black Prairie and Lower Coastal Plains regions of Alabama, *C. cherokeensis* is reported to displace desirable forage species in poor quality pastures (Burns & Buchanan, 1967; Burns et al., 1969). *Carex cherokeensis* persists and spreads in the early spring or late fall by extensive rhizomes when many pasture grasses are dormant. It is more prevalent in poorly managed pastures lacking herbicide applications, and mowing alone is not effective in *C. cherokeensis* control.

Carex longii Mack. is weedy along roadsides and in lawns and flowerbeds (Bryson, 1985a). Unlike most *Carex*, *C. longii* flowers and fruits throughout the frost-free months. Frequently in the southeastern U.S.A., establishment of this species occurs following dispersal of pine bark mulch around shrubs and in flowerbeds suggesting contamination by *C. longii* seeds. From flowerbeds, *C. longii* can invade surrounding areas; however, it is not as aggressive as several invasive *Cyperus* and *Kyllinga* spp. in lawns, turf, gardens, and row crops (Bryson, pers. obs.). Listing of *C. albolutescens* Schwein. as a weed (WSSA, 1989) may be due to taxonomic confusion recently clarified by Rothrock (1991). Although *C. albolutescens* may be locally common, it is not weedy along roadways and in lawns, pastures, and flowerbeds like *C. longii*.

Non-native *Carex* species have become invasive weeds in natural areas through accidental introduction or escape from cultivation as ornamentals. On sandy beaches and dunes, *C. kobomugi* Ohwi, native to Japan, has become an invasive weed along Atlantic coasts (Standley, 1983). It was first collected in the U.S.A. in 1929 (Fernald, 1930), but at that time, it was misidentified as the closely related species *C. macrocephala* Willd. ex Spreng. Since 1929, *C. kobomugi* has spread on sandy beaches from Rhode Island southward to North Carolina and displaced native vegetation and altered the structure of beaches (Small, 1954; Svenson, 1979; Stalter, 1980; Standley, 1983). Its range is likely to expand (Mastrogiuseppe, 2002) despite current eradication efforts in several states. Following introduction as an ornamental, *C. pendula* has recently escaped into natural areas and is beginning to appear on roadsides and stream banks; however, its potential as an invasive weed is unknown (Reznicek, 2002).

Some *Carex* species native to one region of a continent have become weedy in other regions of the same continent. Northern and eastern records of *C. oklahomensis* are most recent, and this sedge may be increasing its range (Standley, 2002). Because *C. oklahomensis* has been frequently collected from recently completed construction sites, it is probably dispersed in hay mulch used for erosion control along roadsides, lakesides, and ditch banks (Bryson et al., 1992a, 1996). *Carex opaca* (F. J. Herm.) P. Rothr. & Reznicek appears to be similarly dispersed (Bryson et al., 1994b).

Seeds and rhizomes of *Carex praegracilis* are dispersed along highways by traffic and by construction and maintenance equipment, and it is sometimes called "tollway sedge" or "freeway sedge" (Swink & Wilhelm, 1979; Bruton & Catling, 1982). *Carex praegracilis* is adapted to extreme environmental conditions (e.g., salty or dry roadsides) and is spreading rapidly eastward and southward from its native range, especially along roadsides where salt is applied for deicing (Reznicek et al., 1976; Bruton & Catling, 1982; Cusick, 1984; Reznicek & Catling, 1987, 2002).

Carex nebrascensis Dewey is listed as a weed (WSSA, 1989; Callahan et al., 1995); it was apparently introduced into Missouri and Illinois, U.S.A., and has become weedy along roadsides (Standley et al., 2002). Heavy infestations of *C. lanuginosa* Michx. were effectively controlled by herbicides, and tillage provided better control of this sedge in light (sandy) soils than in heavier (silt or clay) soils in New Mexico, U.S.A. (Hollingsworth, 1969).

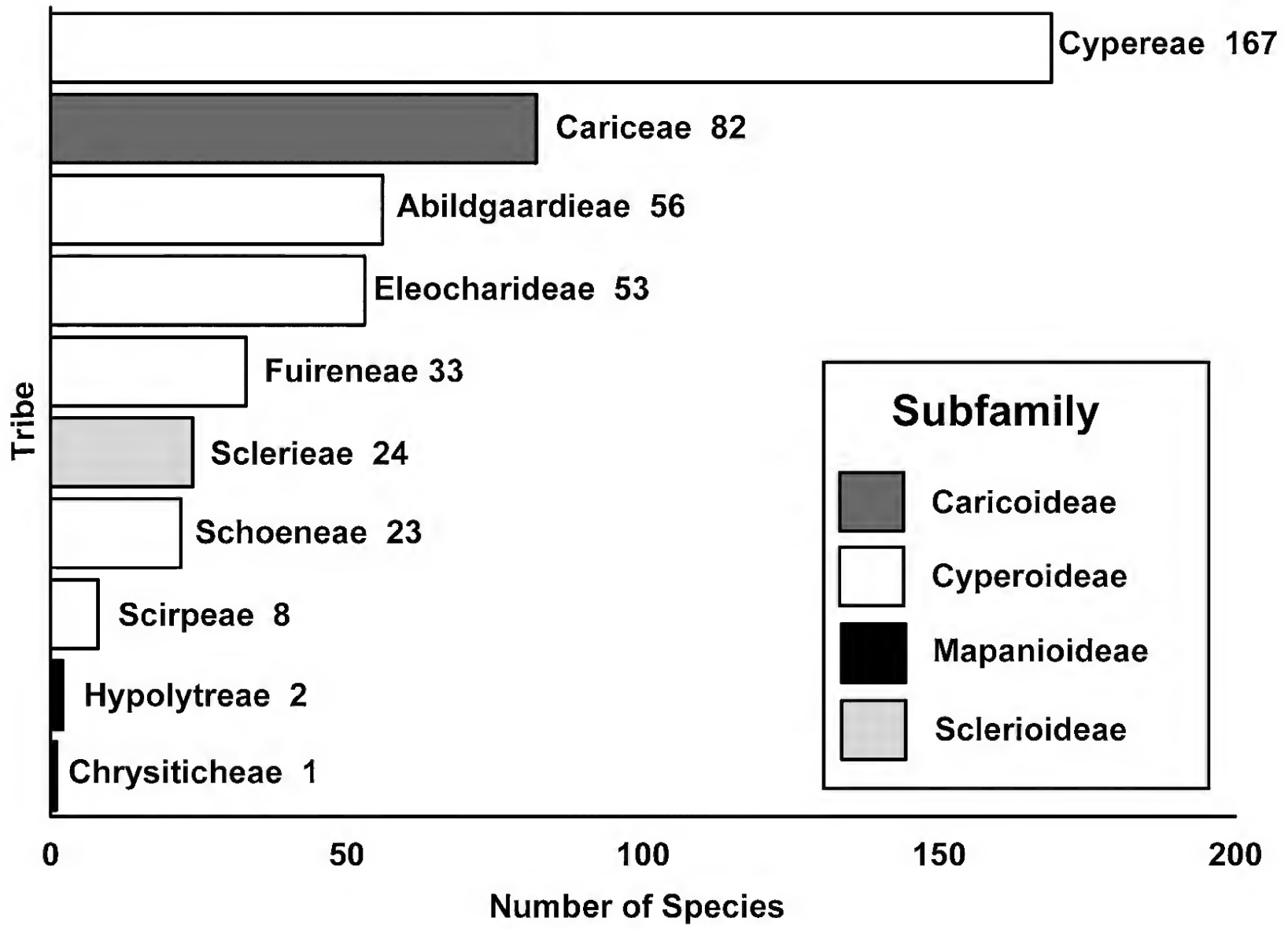

Figure 5. Number of cyperaceous weeds by tribe; classification follows Goetghebeur (1998).

Carex aquatilis Wahlenb., *C. atherodes* Spreng., *C. glaucescens* Elliott, *C. frankii* Kunth, *C. lacustris* Willd., *C. lasiocarpa* Ehrh., *C. louisianica* L. H. Bailey, *C. pallescens* L., *C. rostrata* Stokes in With., *C. senta* Boott, and *C. verrucosa* Muhl. are listed as weeds by the WSSA (WSSA, 1989), while *C. lupulina* Muhl. ex Willd. is listed as a weed by WSSA (1989) and Callahan et al. (1995). *Carex comosa* Boott is considered weedy by Callahan et al. (1995). The U.S. Fish and Wildlife Service (USFWS) (1988) lists *C. comosa* as an obligate wetland species. According to Bernard and Seischab (1994), *C. comosa* invades gaps in wetlands and persists for up to a decade while producing seeds that are dispersed into new gaps. Treated in *Flora of North America* as distinct from *C. frankii*, *C. aureolensis* Steud. (Ford & Reznicek, 2002) is weedy in the southeastern U.S.A. in pastures and along wet roadsides and agricultural field borders. *Carex heterostachya* Bunge and *C. rigescens* (Franch.) V. Krecz. are reported as weeds in China along roadsides and field borders or in orchards and nursery gardens (Zhirong et al., 1990).

CLADIUM

There are four species of *Cladium* worldwide with three in North America (Tucker, 2002a), of which two, *C. jamaicense* Crantz and *C. mariscoides* (Muhl.) Torr., are cited as weeds (Holm et al., 1979; WSSA, 1989). Both of these wetland species occur in the U.S.A. *Cladium jamaicense* (saw grass) inhabits marshes near the coast and is the predominant species of the Everglades marshes of southern Florida, U.S.A. (Steward & Ornes, 1975; Godfrey & Wooten, 1979). Much of this formerly vast marshland has been drained for flood control and converted into agricultural fields for the cultivation of sugarcane and other crops (Godfrey & Wooten, 1979). In such an altered and unnatural landscape, *C. jamaicense* is viewed as an impediment to drainage and navigation and a hindrance to agriculture.

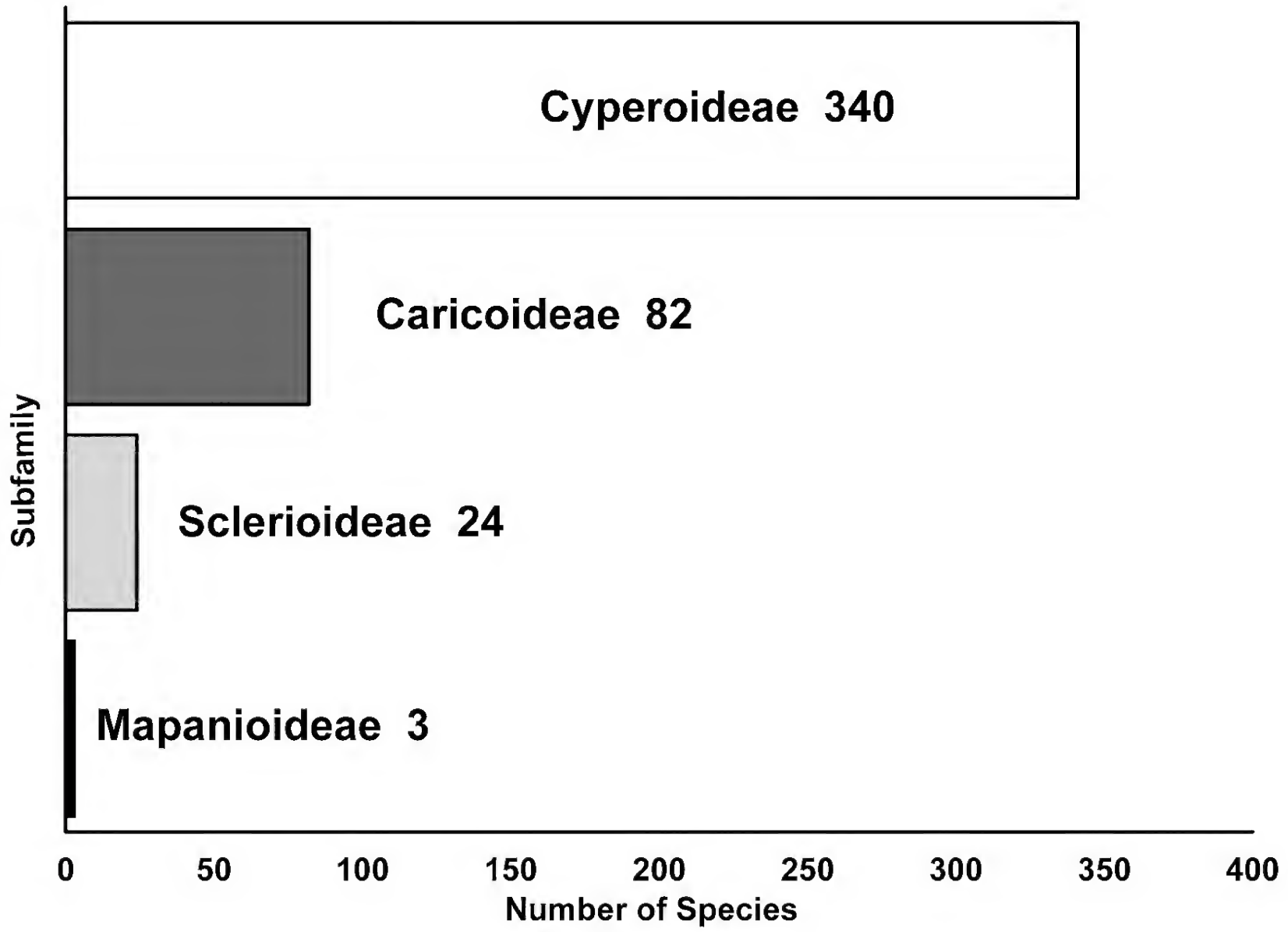

Figure 6. Number of cyperaceous weeds by subfamily; classification follows Goetghebeur (1998).

However, a massive venture is currently underway (U.S. Army Corps of Engineers, 1999) to reverse the damage done by drainage projects of the past and to reclaim portions of the Everglades ecosystem, which if successful will also restore the natural habitat of *C. jamaicense*, taking it from weed to its former status as the predominant plant of its natural community. Weediness is oftentimes an artifact of human perception and folly.

COURTOISINA

Courtoisina Soják is a small genus of two species found in Africa, Madagascar, India, and southeastern Asia (Haines & Lye, 1983; Gordon-Gray, 1995; Vorster, 1996; Mabberley, 1997). *Courtoisina cyperoides* (Roxb.) Soják was cited as a weed in rice fields (Simpson & Koyama, 1998; Simpson & Inglis, 2001) and has also been reported from wet mud of freshwater pans, seasonally wet grasslands, and temporary pools (Haines & Lye, 1983; Gordon-Gray, 1995).

CYPERUS

There are about 600 species of *Cyperus* worldwide (Tucker et al., 2002). In terms of their significance as weeds, *Cyperus* species are by far the most important in Cyperaceae. Appendix 2 lists 147 species of *Cyperus* that have been cited as weeds. The adverse economic impact of *Cyperus* is great. According to Holm et al. (1977), it contains the world's worst weed and three additional species listed among the 33 worst agricultural weeds in the world. The most recent comprehensive, universal treatment of *Cyperus* was by Kükenthal (1935–1936), who defined the genus broadly as consisting of six subgenera: *Cyperus*, *Mariscus* (Vahl) C. B. Clarke, *Torulinium* (Desv.) Kük., *Juncellus* (C. B. Clarke) C. B. Clarke, *Pycreus* (P. Beauv.) A. Gray, and *Kyllinga*. *Cyperus* is taxonomically complex, and the status of its subgenera is widely disputed even among contemporary workers (cf. Kern, 1974; Haines & Lye, 1983; Koyama, 1985; Lye, 1992; Wilson, 1993; Adams, 1994; Gordon-Gray, 1995;

Muasya et al., 2000a, b, 2002; Tucker et al., 2002). Although we question the apparent inconsistency in segregating *Kyllinga* and not *Pycreus* and *Juncellus*, herein we pragmatically adopt the generic taxonomy in *Flora of North America*, Vol. 23 (Tucker et al., 2002). Recent molecular evidence seems to support a broad circumscription of *Cyperus* to include *Kyllinga*, *Pycreus*, and other segregate genera (Muasya, 2002).

To varying degrees, the following characteristics undoubtedly contribute to the aggressive, invasive tendencies of *Cyperus* spp. and other sedges: large numbers of small, readily dispersed achenes; vegetative reproduction; longevity of tubers, rhizomes, or other subterranean structures; production of allelopathic compounds; paucity of pathogens; short life reproductive cycle, especially in annual species; tolerance of broad ranges of environmental conditions; C_4 photosynthesis; and resistance to control with herbicides and cultural methods, including tillage.

Cyperus rotundus is considered the world's worst weed because of its ability to survive, spread, and compete, especially in agricultural areas (Holm et al., 1977; Terry, 2001). It was reported in 52 crops and 92 countries (Holm et al., 1977, 1979, 1997). In the U.S.A., Elliott (1821) described *C. rotundus* (*C. hydra* Michx.) as a "scourge" of plantations in Georgia and South Carolina and recommended daily tilling of the soil for control. The infraspecific taxonomy of this cosmopolitan weed is extremely complex and in need of revision (cf. Kükenthal, 1935–1936). In addition to threatening agriculture, *C. rotundus* is a troublesome weed in urban areas and natural communities after disturbance. Although it rarely sets viable seeds (Holm et al., 1977; Thullen & Keeley, 1979), *C. rotundus* produces numerous rhizomes that reportedly can penetrate and grow through fleshy subterranean organs of root crops and even asphalt pavement (Hauser, 1962a, b; Thullen & Keeley, 1979). These rhizomes form tubers that give rise to new aerial plants or produce other rhizomes or they may remain dormant during periods of adverse environmental conditions including heat, cold, drought, flooding, or inadequate aeration (Ranade & Burns, 1925; Williams, 1978; Bendixen & Nandihalli, 1987; Wills, 1987; Miles et al., 1996). The tubers of *C. rotundus* are bitter, rough, and are often connected serially by rhizomes with or without giving rise to new plants (Plowman, 1906; Ranade & Burns, 1925; Hauser, 1962a; Wills & Briscoe, 1970; Holm et al., 1977; Wills, 1987). Dormant tubers make *C. rotundus* difficult to control in turf, and only a few selective herbicides that effectively control sedges are approved for use in turf or in row crops (Aleixo & Valio, 1976; Keeley, 1987; Pereira et al., 1987; Holt & Orcutt, 1996). Tubers and rhizomes of *C. rotundus* produce allelopathic compounds that reduce growth in crops such as cotton (Martinez-Diaz, 1997).

Diagnostic features of *Cyperus rotundus* include abruptly tapering leaves, inflorescence bracts equaling or longer than the inflorescence, and purplish floral scales (Wills & Briscoe, 1970; Horowitz, 1972; Wills, 1987). In a comparative study of *C. rotundus* morphology based on collections from 13 states in the U.S.A. and 21 locations from around the world, Wills (1998) detected differences in numbers of shoots produced by single tubers, numbers of leaves per shoot, lengths and widths of leaves, lengths of culms, flowering times during the year, numbers and lengths of rachises, lengths of rachillae and spikelets, and numbers, lengths, and widths of involucral bracts. Infraspecific variation in *C. rotundus* is also documented in Ceylon (Koyama, 1985), East Africa (Haines & Lye, 1983), and Natal Province (now KwaZulu-Natal Province), South Africa (Gordon-Gray, 1995). Although these differences occurred within some traits on a worldwide basis, the basic characteristics distinguishing *C. rotundus* from other taxa were consistent (Wills, 1998) and differed from closely related taxa such as *C. bifax* C. B. Clarke. Worldwide, *C. rotundus* is a troublesome weed in corn (*Zea mays* L.), cotton, peanut (*Arachis hypogaea* L.), rice, sorghum (*Sorghum vulgare* Pers.), soybean, sugarcane (*Saccharum officinarum* L.), turf grass species, and many other vegetable, nursery, row, rotation, and plantation crops (Long et al., 1962; Bryson, 1985b; Bendixen & Nandihalli, 1987; Holt & Orcutt, 1991; Derr & Wilcut, 1993; Grichar et al., 1992; Wills, 1998; Bryson et al., 2002, 2003b).

Cyperus esculentus is ranked as the world's 16th worst weed (Holm et al., 1977). Highly variable and widely distributed in tropical, subtropical, and temperate regions around the world, its infraspecific taxonomy was revised by Schippers et al. (1995). Schippers et al. (1993) attribute invasiveness in *C. esculentus* to an increase in the rate of population

growth brought about by tillage. *Cyperus esculentus* has rhizomes and tubers (Thumbleson & Kommedahl, 1961; Jansen, 1971; Stoller et al., 1972); however, its rhizomes are fleshy and terminate in a sweet-tasting tuber (Garg et al., 1967). Additional diagnostic characters include gradually tapering, acute leaves, yellow to yellowish orange floral scales, and bracts longer than the inflorescence. *Cyperus esculentus* is pernicious and difficult to control in agricultural and urban areas. Although it produces seeds more frequently than *C. rotundus* (Wills, 1987), *C. esculentus* reproduces primarily from tubers (Thumbleson & Kommedahl, 1961). *Cyperus esculentus* tubers remain dormant for prolonged periods during adverse environmental conditions and only produce tubers from rhizomes of the parent plant (Wills, 1987). *Cyperus esculentus* is able to survive colder winter conditions than *C. rotundus* and thus is more widespread worldwide (Stoller & Sweet, 1987; Wills, 1987). The tubers of *C. esculentus* are called chufas, tiger nuts, or rush nuts (Abad et al., 2000; DeFelice, 2002). *Cyperus esculentus* is often planted for its tubers that provide food for deer, turkey, wild hogs, and other animals (Miller & Miller, 1999; Abad et al., 2000; DeFelice, 2002). Humans also use the tubers as food for domesticated animals (e.g., chickens, swine) and directly consume them as food, use them as a spice, and use them to prepare a drink called "horchata de chufas" (Zeven & Zhukovsky, 1975; Darby et al., 1977; Allan, 1978; DeFilipps, 1980c; Negbi, 1992; Stephens, 1994; Bryson et al., 1998). Unfortunately, the tubers used by humans contribute to the invasive character of *C. esculentus* and to its dispersal. In addition to the crops mentioned above for *C. rotundus*, *C. esculentus* is also a principal weed of potato (*Solanum tuberosum*), sugarbeet (*Beta vulgaris* L.), and many cool-season crops (Bendixen & Nandihalli, 1987).

Cyperus difformis and *C. iria* are ranked 32nd and 33rd among the world's worst weeds, respectively (Holm et al., 1977). Both are caespitose annuals and often produce clumps of many culms and have become established in tropical and temperate areas of the world. In the southeastern U.S.A., *C. difformis* and *C. iria* are primarily weeds of drainage ditches, rice fields, and poorly drained sites in other agricultural fields or disturbed areas. *Cyperus difformis* and *C. iria* produce multiple generations per year under optimal growing conditions and in the tropics flower and produce seeds year-round (Holm et al., 1977). *Cyperus difformis* can complete its life cycle every four to six weeks throughout the growing season (Holm et al., 1977). A single plant of *C. iria* may produce more than 5000 viable seeds, while an individual of *C. difformis* can produce 50,000 seeds with a germination rate of 60% or more (Jacometti, 1912). Short generation times and high seed production favor rapid dispersal (Vaillant, 1967), large seed reservoirs in the soil, high population levels (Holm et al., 1977; Bryson, 1984), and an increased potential for the development of herbicide resistance. In rice-production areas of California, multiple *C. difformis* generations per year and large seed production may be primary factors in the rapid development of herbicide resistance to bensulfuron (Pappas-Fader et al., 1993, 1994; Hill et al., 1994). Despite similarities in habitat and growth and reproductive patterns, *C. difformis* is C_3 and *C. iria* is C_4 (Hesla et al., 1982).

Cyperus rotundus, *C. esculentus*, *C. difformis*, and *C. iria* are all suspected to have originated in Asia. Other *Cyperus* spp. of probable Asian origin include *C. compressus*, *C. haspan*, *C. pilosus*, and *C. sanguinolentus* (Holm et al., 1979). All are naturalized weeds in other regions of the world (Bryson & Carter, 1995; Carter & Bryson, 2000b).

Cyperus haspan is among the world's worst weeds (Holm et al., 1997). It has been reported as a weed in 12 crops and 39 countries throughout tropical and semitropical areas of Africa, Asia, Australia, South America, and North America (Lin, 1968; Holm et al., 1977, 1979; Kissmann, 1997). *Cyperus haspan* is a recent introduction into Hawaii with the first collection made in 1957 (Wagner et al., 1990). An individual plant can produce more than 50,000 achenes per year (Datta & Banerjee, 1976), and although plants produce achenes during the first season of growth, they do not form rhizomes until the second year (Tadulingam & Venkatanaryana, 1955). *Cyperus haspan*, a C_3 plant, commonly occurs in shallow standing water and germinates and grows well in wet, sandy, acidic soils (Bertels, 1957; Eyles & Robertson, 1963; Dirven, 1970). *Cyperus haspan* is sometimes broken into two subspecies; *C. haspan* subsp. *juncoides* (Lam.) Kük. is a taller plant with conspicuous rhizomes (Kükenthal, 1935–1936; Kern, 1974; Koyama, 1985). *Cyperus haspan* is sometimes confused with closely related *C. tenuispi-*

ca Steud., a species with more widely spaced floral scales, and both species are cited as frequent weeds in rice fields in Asia (Kern, 1974; Koyama, 1985).

Cyperus entrerianus is native to temperate regions of South America; it is also known from the Caribbean, Mexico, and the Coastal Plain of the southern U.S.A. (Kükenthal, 1935–1936; Barros, 1960; Carter, 1990; Tucker, 1994). In his comprehensive revision of *Cyperus*, Kükenthal (1935–1936) accorded specific rank to *C. entrerianus*; however, Barros (1960) reduced it to varietal status under *C. luzulae* (L.) Rottb. ex Retz., and Denton (1978) gave it no rank, treating it as a synonym of *C. luzulae*. Carter (1990) and subsequent authors (Tucker, 1994; Tucker et al., 2002) treated this taxon at the rank of species. In the southeastern U.S.A., flooding, construction equipment, mowing, and soil-moving activities, especially along highways, disperse the small achenes of *C. entrerianus*, resulting in infestations in a variety of disturbed habitats (Carter, 1990; Carter & Bryson, 1996). *Cyperus entrerianus* displaces native vegetation even in undisturbed habitats, and, without widespread control, it will likely continue to spread rapidly, infesting agricultural, forested, riparian, and urban areas. Figure 4 shows the dispersal of *C. entrerianus* in the U.S.A., where by 2003 it was documented in 43 counties from Florida and southern Georgia into southeastern Texas. In the southern U.S.A., *C. entrerianus* reproduces copiously from achenes and spreads vegetatively and perennates from short rhizomes. *Cyperus entrerianus* is a prolific seed producer, with the number of seeds per inflorescence ranging from 1000–20,000+ depending on the size and maturity of plants and mature plants (> 1 year old) producing 10–100+ inflorescences per year (Carter & Bryson, 1996; Bryson et al., 2003a). Preliminary seed germination studies indicate moderate to high viability (55%–95%) (Carter & Bryson, 1996). In the southeastern U.S.A., *C. entrerianus* flowers and fruits from June until frost in November or December (Carter, 1990; Carter & Jones, 1991; Bryson & Carter, 1994). *Cyperus entrerianus* continues to spread at an alarming rate and threatens agricultural and natural areas. Also, preliminary studies suggest that populations will potentially spread northward into Arkansas, North Carolina, South Carolina, Tennessee, and Virginia. Additional research is needed to determine more effective methods of prevention and control.

Cyperus acuminatus Torr. & Hook., *C. eragrostis*, *C. luzulae*, *C. ochraceus*, *C. pseudovegetus*, *C. reflexus*, *C. surinamensis*, and *C. virens* are cited as weeds (Appendix 2) and are classified with *C. entrerianus* in *Cyperus* sect. *Luzuloidei* Kunth (Kükenthal, 1935–1936; Denton, 1978). *Cyperus acuminatus*, *C. pseudovegetus*, and *C. virens* are all native to North America, where they are currently relatively minor weeds; however, they could become problems if introduced beyond their native ranges. *Cyperus pseudovegetus* is widely distributed in eastern North America (Denton, 1978; Tucker et al., 2002). In the U.S.A., *C. pseudovegetus* and *C. virens* are common in disturbed, intermittently wet soils, e.g., roadside ditches, margins of ponds, and swales in fields, pastures, and grasslands. *Cyperus virens* is widely distributed in the New World, ranging from South America, Central America, the Caribbean Islands, Mexico, and the southern U.S.A. (Denton, 1978), and is recently introduced into Hawaii with the first collection made in 1976 (Wagner et al., 1990). Several infraspecific taxa have been recognized (Denton, 1978), including *C. virens* var. *drummondii*. Carter et al. (1999) showed that *C. drummondii* is specifically distinct from *C. virens* and in the southeastern U.S.A. has a more restricted distribution and habitat and is less weedy than *C. virens*. *Cyperus reflexus* occurs in temperate South America, Central America, Mexico, and in the U.S.A. (Denton, 1978; Tucker, 1994). It is introduced in Australia, where it is naturalized near Sydney (Wilson, 1993). In the U.S.A., *C. reflexus* is most common in southeastern Texas and Louisiana, where it is found in intermittently wet, disturbed soils of ditches, fields, and grasslands (Denton, 1978; Carter, pers. obs.); it has also been reported in western Florida (Wunderlin, 1998). Additional research is needed to elucidate the relationship between *C. fraternus* Kunth and *C. reflexus*, which has been treated as *C. reflexus* var. *fraternus* (Kunth) Kuntze (Kükenthal, 1935–1936; Denton, 1978). *Cyperus ochraceus* is widespread in the New World and is known from South America, Central America, Mexico, the U.S.A., and the Caribbean Islands (Denton, 1978). It is currently only a minor weed in the southern U.S.A., where it is found in disturbed, intermittently wet soils and is most common in Texas and Louisiana but has dispersed to scattered sites elsewhere (Denton, 1978; Tucker et al., 2002; Carter, pers. obs.).

Cyperus surinamensis is widely distributed in the New World, ranging from South America, Central America, Mexico, and the Caribbean Islands into southeastern and south-central U.S.A. (Denton, 1978). Readily identified by its retrorsely scabrid culms, *C. surinamensis* has been cited as a weed in both North and South America (WSSA, 1989; Kissman, 1997). In warmer parts of the southeastern U.S.A., it is a common weed in a variety of open disturbed sites with hydric soils.

Cyperus eragrostis occurs naturally in South America and in California, Oregon, Washington, and British Columbia in North America (Denton, 1978). It has been used ornamentally, which in part accounts for its introduction into other parts of the world (Tucker, 1987; Sell & Murrell, 1996; Darke, 1999; Petřík, 2003). It occurs sporadically in the eastern U.S.A., where it is introduced and appears to be spreading (Bryson & Carter, 1994; Bryson et al., 1996; Tucker et al., 2002). *Cyperus eragrostis* is naturalized in Australia and has expanded its range and frequency there, where it is a weed of rice and ephemerally wet, disturbed sites (Wilson, 1993). In reporting *C. eragrostis* new to the Czech Republic, Petřík (2003) provides a thorough account of its invasion of Europe, where it is widely distributed and has been known since the mid-1800s. Given its association with rice as a weed in Australia, *C. eragrostis* could become a problem in rice agriculture in the southeastern U.S.A. and elsewhere. Additional research is needed to determine more about the distribution and dispersal of *C. eragrostis*, its potential to become an agricultural pest, and its control.

Cyperus oxylepis Nees ex Steud. and *C. elegans* L. are widely distributed in tropical, subtropical, and warm temperate regions of the New World. Both species have viscid foliage and are markedly aromatic, with the fragrance of cedar wood (*Juniperus virginiana* L.) sometimes sensed in the field before the plants are seen. The floral scales of *C. oxylepis* are golden brown and those of *C. elegans* are greenish tan. *Cyperus oxylepis*, listed as a weed (WSSA, 1989), is apparently expanding its range in coastal areas of the southeastern U.S.A. (O'Neill, 1938b; Thieret, 1964; Tucker, 1987; Bryson & Carter, 1992; Bryson et al., 1996), where it is found in disturbed clay soils of salt marshes.

A number of aquatic *Cyperus* species cultivated in ponds and water gardens have become naturalized. All have the potential to become invasive weeds in aquatic and wetland habitats in tropical and subtropical areas, and at least one, *C. prolifer*, is invasive in the U.S.A. (Carter et al., 1996). Trade and importation of these species should be carefully regulated to prevent further impact. *Cyperus alternifolius* subsp. *flabelliformis* has been used as an ornamental in water gardens and as a potted plant for more than 200 years (Bailey & Bailey, 1976) and is widely naturalized from cultivation in the tropics and subtropics and other warm areas (Bailey, 1935, 1949; O'Neill, 1946; Kern, 1974; DeFilipps, 1980c; Koyama, 1985; Wagner et al., 1990; Sell & Murrell, 1996). It has been variously known as *C. alternifolius* subsp. *flabelliformis* Kük.; *C. flabelliformis* Rottb., nom. illeg.; and *C. involucratus* Rottb. In the U.S.A. it is naturalized in Florida, Louisiana, Texas, and California, where it is occasionally found in moist to hydric soils of roadside ditches, stream banks, vacant lots, and other disturbed sites (Carter, pers. obs.; Tucker et al., 2002). In his worldwide monograph of *Cyperus*, Kükenthal (1935–1936) recognized two subspecies: *C. alternifolius* subsp. *alternifolius* and *C. alternifolius* subsp. *flabelliformis*. Baijnath (1975) treated these as species and stated that *C. alternifolius* is rare and mostly restricted to Madagascar where it is native and that *C. involucratus* [= *C. alternifolius* subsp. *flabelliformis*] is the correct name for the widely naturalized cultivated plant indigenous to Africa. More recently, Gordon-Gray (1995) adopted Kükenthal's taxonomy, indicating the need for additional critical investigation of this complex in southern Africa, which also includes the related cultivated aquatics *C. sexangularis* and *C. textilis*. Until further research elucidates the relationships among these taxa, we have adopted the more conservative taxonomy of Kükenthal (1935–1936) and Gordon-Gray (1995), recognizing two subspecies within *C. alternifolius*. Although popular in water gardens in southern Africa, *C. sexangularis* survives under drier conditions in the absence of extended water stress (Gordon-Gray, 1995), and *C. textilis* is naturalized in the Azores (DeFilipps, 1980c). Thus, it would appear that *C. alternifolius*, *C. sexangularis*, and *C. textilis* have the potential to become invasive pests in a variety of aquatic, wetland, and terrestrial habitats in tropical and subtropical regions.

Cyperus prolifer is sold as an ornamental for water gardens (Bailey & Bailey, 1976; Simpson, 1994) and has been variously listed as *Cyperus has-*

pan cv. 'viviparus' (Watkins & Sheehan, 1975; Graf, 1985), *C. papyrus* cv. 'nanus' (Bailey & Bailey, 1976), and *C. isocladus* Kunth (Bailey & Bailey, 1976; Everett, 1980–1982). It has been confused with *C. haspan*, from which it is readily distinguished by its thick rhizome and inflorescence of 50 to 100 rays of more or less uniform length. *Cyperus prolifer* is indigenous to eastern Africa where it inhabits marshes, marshy shores, and swampy stream banks (Kükenthal, 1935–1936; Haines & Lye, 1983). Although Simpson (1994) stated that it was not a weed, *C. prolifer* has become naturalized from cultivation in the U.S.A. in central Florida where it has invaded the margins of lakes (Carter et al., 1996) and in Hawaii (Strong & Wagner, 1997). In Florida, *C. prolifer* grows in floating mats and along margins of natural limesink lakes, where it is associated with *Oxycaryum cubense* (Carter et al., 1996). One extensive population of *C. prolifer* in Lake Huntley, Florida, was established after dispersing from an adjacent water garden during eight years of cultivation (Carter et al., 1996).

Cyperus papyrus is a remarkable plant. Because of its use in the manufacture of the first paper by the ancient Egyptians, it is perhaps the best known of the sedges (Schery, 1972). It is found in central and southern Africa and the Nile River valley and is naturalized in Sicily (Kükenthal, 1935–1936; DeFilipps, 1980c; Gordon-Gray, 1995). *Cyperus papyrus* forms dense stands in aquatic and wetland habitats and dominates swamps with low biodiversity in northern Uganda (Mabberley, 1997). Plants may grow to 5 m high, making it one of the largest sedges (Koyama, 1985), and it is cultivated as an ornamental and curiosity in greenhouses and outdoors in ponds and water gardens in tropical and subtropical regions of the world (Bailey, 1935, 1949; Bailey & Bailey, 1976). *Cyperus papyrus* is naturalized in Florida, U.S.A. (Wunderlin, 1998), where it is evidently not yet invasive, but would appear to have the potential to invade aquatic and wetland habitats in tropical and subtropical areas given its dominance in swamps of northern Uganda.

Cyperus alopecuroides is a widely distributed aquatic sedge in tropical and subtropical regions of the Old World, e.g., northern and tropical Africa, Madagascar, India, Ceylon, Indo-China, Malaysia, and northern Australia; in the New World it is known only from Guadeloupe in the West Indies and Florida, U.S.A. (Kükenthal, 1935–1936; Koyama, 1985; Carter et al., 1996). It is a robust plant to 1.5 m high and in its habit and general inflorescence pattern resembles the tropical species *C. imbricatus* Retz. Both taxa were placed in section *Exaltati* Benth. by Kükenthal (1935–1936). Its size in combination with other characters make *C. imbricatus* a striking plant in the field: broad bracts and leaf blades (to 15 mm wide) with contrasting surfaces (adaxial light green, abaxial glaucous), and a branched inflorescence with spikes of densely clustered golden-brown spikelets (Carter et al., 1996). Although it seems to be more clearly allied with subgenus *Cyperus* (Kükenthal, 1935–1936; Koyama, 1985), it has characteristics that seem to defy placement there: namely, a bicarpellate gynoecium with two stigmas and a lenticular achene with face adjacent to rachilla. When taken alone, the gynoecium and fruit characteristics seem to indicate a relationship with subgenus *Juncellus* (Clarke, 1908); however, both bi- and trigynous pistils have been found in the same inflorescence (Koyama, 1985), which supports inclusion in subgenus *Cyperus*. In central Florida, where this emergent aquatic sedge was probably introduced with nursery stock used to revegetate a reclamation wetland in an abandoned phosphate pit, *C. alopecuroides* exhibits invasive characteristics, forming extensive stands in shallow water and floating mats (Carter et al., 1996). According to Kantor (1999), *C. alopecuroides* was cultivated by the ancient Egyptians and its inflorescence was widely depicted in one of the characteristic motifs of their decorative art. Additional research on *C. alopecuroides* is needed to understand better its potential for becoming an invasive weed and its phylogenetic relationships.

Cyperus odoratus is widely distributed in tropical and subtropical regions around the world (Kükenthal, 1935–1936; Kern, 1974) and is generally found in disturbed hydric soils and wetlands. It is frequently cited as a weed and has been listed as a pest of rice (Appendix 2). In the southeastern U.S.A., *C. odoratus* is commonly found in wet disturbed sites, e.g., ditches, stream banks, swamps, wetlands, and edges of ponds, but it is not of major economic importance. *Cyperus odoratus* is classified in subgenus *Diclidium* (Schrad. ex Nees) C. B. Clarke [= *Torulinium*] characterized by spikelets that disarticulate into one-fruited segments (Kükenthal,

1935–1936), and its achenes, enclasped within corky rachilla segments, are dispersed by water (Kern, 1974; Haines & Lye, 1983). Jones et al. (1996) recognized several infraspecific taxa of this variable species in North America. In the U.S.A., *C. odoratus* is frequently associated with *C. erythrorhizos* Muhl., which is also listed as a weed (Holm et al., 1979; WSSA, 1989). *Cyperus erythrorhizos*, a widespread annual sedge restricted to North America (Kükenthal, 1935–1936; Tucker et al., 2002), inhabits disturbed hydric soils of wetlands, ditches, stream banks, floodplains, edges of ponds and swamps, swales in fields and pastures, and occasionally rice fields. It is of minor economic importance. *Cyperus digitatus* Roxb. is closely related to *C. erythrorhizos*, but it is perennial and generally a much larger plant. *Cyperus digitatus* is widely distributed in tropical and subtropical regions of both the Eastern and Western hemispheres (Kükenthal, 1935–1936; Kern, 1974; Koyama, 1985) and, as can be seen in Appendix 2, is frequently cited as a weed. Because it is much more wide-ranging and cited as a pest of rice in the Eastern Hemisphere (Kern, 1974), *C. digitatus* is probably of greater economic significance than *C. erythrorhizos*.

Cyperus articulatus L. ranges widely in tropical, subtropical, and warm temperate regions around the world (Kükenthal, 1935–1936). It is a rhizomatous perennial with a reed-like habit, septate culms, and bladeless (usually) leaves. In the southeastern U.S.A., *C. articulatus* occurs near the coast in marshes, ditches, or other open disturbed sites, and populations usually appear as scattered, solitary aerial stems. As shown in Appendix 2, *C. articulatus* is widely reported as a weed (Holm et al., 1979; Kühn, 1982; WSSA, 1989; Kissman, 1997).

Cyperus compressus is widely distributed in tropical, subtropical, and warm temperate regions around the world (Kükenthal, 1935–1936). It is frequently cited as a weed and is found in a variety of habitats disturbed and altered by humans, e.g., waste places, grasslands, lawns, crops, roadsides, fallow rice fields (Ohwi, 1965; Lin, 1968; Kern, 1974; Kühn, 1982; Koyama, 1985; WSSA, 1989; Ravi & Mohanan, 2002). In warmer parts of the southeastern U.S.A., it is a common weed in sandy loam soils of agricultural fields, roadsides, gardens, and other disturbed sites. According to Bailey (1935) and Huxley (1992), *C. compressus* has been cultivated as an ornamental, which probably partly accounts for its wide distribution.

Cyperus pilosus is a weed of tropical, subtropical, and warm temperate areas in Asia, western Africa, and Australia (Kükenthal, 1935–1936; Koyama, 1985; Wilson, 1993) and is commonly cited as a weed of rice (McGivney, 1938; Kern, 1974; Wagner et al., 1990). It has been collected in Hawaii, where it was possibly introduced with rice agriculture, but has not been found there since 1916 (Wagner et al., 1990). *Cyperus pilosus* has been known in the southeastern U.S.A. since 1938, where it was probably introduced through the cultivation of rice (McGivney, 1938; O'Neill, 1938a). In the southeastern U.S.A., it is found in rice fields, wet ditches, and other wet disturbed sites and is apparently spreading, having been reported new to several states in recent years (Burkhalter, 1985; Bryson & Carter, 1992; Tucker et al., 2002). *Cyperus procerus* Rottb. is related to *C. pilosus*. It is known from tropical and subtropical regions of western Africa, India, Asia, Malaysia, and Australia (Koyama, 1985; Wilson, 1993) and has been cited as a weed of rice fields in Asia and western Africa (Hooper & Napper, 1972; Kern, 1974). *Cyperus pilosus* and *C. procerus* share several characteristics that distinguish them from most other *Cyperus* spp.: stoloniferous habit, triquetrous culm, and hispidulous rachis.

Cyperus sphacelatus Rottb. is widely distributed in the tropics and subtropics from eastern Africa, Ceylon, Malaysia, northern Australia (Queensland), Tahiti, South America, Central America, and the Caribbean (Clarke, 1900; Uittien, 1932; Kükenthal, 1935–1936; Haines & Lye, 1983; Tucker, 1983; Koyama, 1985). It is a heliophyte of moist disturbed sites, beaches, riverbanks, fields, and roadsides (Reed, 1977; Tucker, 1983; Carter et al., 1996), and, in Malaysia, *C. sphacelatus* is reportedly a common weed on airstrips (Kern, 1974), which suggests dispersal via air traffic. Mohr (1901) reported *C. sphacelatus* from ballast heaps in Mobile, Alabama, U.S.A., and more recently naturalized populations have been found in southern Florida, U.S.A. (Carter et al., 1996). An analysis of floral scale length on herbarium specimens indicates that the populations in Florida probably originated from the West Indies (Carter et al., 1996). The recent discovery of naturalized populations in peninsular Florida suggests that *C. sphacelatus* is currently

undergoing range expansion in the southeastern U.S.A. Field botanists and weed scientists should be vigilant to detect additional populations of this introduced pest, and appropriate governmental agencies should initiate measures to survey for and eradicate populations of *C. sphacelatus* in the U.S.A. before it spreads further. The following combination of characteristics distinguishes *C. sphacelatus* from other *Cyperus* spp.: annual caespitose habit, triquetrous achene, diffuse inflorescence with flattened spikelets, and variegated floral scales pale, nearly white, each with two conspicuous reddish patches.

Cyperus distans L. f. is a pantropical weed of marshes, canal banks, ditches, agricultural crops, and grasslands in Africa, India, Sri Lanka, southeastern Asia, Malaysia, southern China, the Philippines, the Caribbean islands, Central America, Mexico, and tropical South America (Clarke, 1900; Uittien, 1932; Kükenthal, 1935–1936; Koyama, 1985; Adams, 1994; Tucker, 1994). *Cyperus distans* is frequently cited as a weed in the Eastern Hemisphere, where aquatic biotypes are known, and it is a pest of rice fields and grasslands (Appendix 2). It occurs sporadically in the southeastern U.S.A. and has been reported from coastal North Carolina, Georgia, and Florida (Small, 1933; Kükenthal, 1935–1936; McGivney, 1938; Radford et al., 1968; Beal, 1977; Carter et al., 1996). The recent report (Carter et al., 1996) from Florida, U.S.A., suggests that *C. distans* is expanding its range there. The following combination of characteristics distinguishes *C. distans* from other *Cyperus* spp.: rhizomes; scales ascending, remote, with 3- to 5-nerved greenish keels, sanguineous to reddish brown nerveless sides, and with scarious emarginate tips. Field botanists and weed scientists should seek and report additional populations, and appropriate state and federal agencies should undertake eradication measures to ensure early control of this potentially invasive pest in the southeastern U.S.A.

A number of species classified by Kükenthal (1935–1936) in *Cyperus* sect. *Umbellati* C. B. Clarke are listed as weeds in Appendix 2. *Cyperus cyperinus* (Retz.) Suringar and *C. cyperoides* (L.) Kuntze are broadly distributed in warm parts of the Eastern Hemisphere (Kükenthal, 1935–1936; Kern, 1974). *Cyperus cyperoides* is introduced in the West Indies (Kükenthal, 1935–1936; Kern, 1974), and *C. cyperinus* has been reported as a wool alien in Great Britain (Sell & Murrell, 1996). Both species have frequently been cited as weeds (Appendix 2). The variation within these species is complex and poorly understood, with numerous infraspecific taxa recognized, and the synonymy is formidable (cf. Kükenthal, 1935–1936; Kern, 1974; Haines & Lye, 1983; Koyama, 1985). No thorough systematic review of this group has been done since Kükenthal (1935–1936). Additional research to elucidate the relationships of infraspecific taxa and their relationships with one another and with related species, e.g., *C. paniceus* Boeckeler, is needed. Such research with North American species of section *Umbellati* has been productive, resulting in substantial taxonomic and nomenclatural clarification (Carter, 1984; Carter & Jarvis, 1986; Carter & Kral, 1990; Carter & Jones, 1997).

Cyperus croceus Vahl, *C. echinatus* (L.) A. W. Wood, and *C. retrorsus* Chapm. are listed as weeds by WSSA (1989). All are caespitose perennials with umbelliform inflorescences of simple spikes of densely clustered spikelets, classified by Kükenthal (1935–1936) in section *Umbellati*. These taxa are native and widely distributed in the southeastern U.S.A., where they are found in lawns, pastures, roadsides, waste places, disturbed woodlands, and other ruderal sites (Carter, 1984). *Cyperus croceus* and *C. echinatus* were long known as *C. globulosus* auct. non Aubl. and *C. ovularis* (Michx.) Torr., respectively (Carter & Kral, 1990). *Cyperus croceus* also occurs in the Caribbean Islands (Carter, 1984). *Cyperus croceus* and *C. echinatus* have been reported as wool aliens in Great Britain (Sell & Murrell, 1996), and *C. croceus* has been associated with ballast (Britton, 1886). *Cyperus echinatus* is reportedly naturalized in the Azores (DeFilipps, 1980c). Carter (1984, in prep.) shows that plants with ascending yellowish scales are distinct from *C. retrorsus* and should be called *C. ovatus* Baldwin. *Cyperus ovatus* is a coastal species in the southeastern U.S.A., which is found in slightly wetter sites than related *C. retrorsus*, e.g., moist ditches, disturbed sites in moist sandy, loamy, or peaty soils in coastal flatwoods (Carter, 1984, in prep.). Although not listed by WSSA (1989), we include the related taxa *C. retroflexus* Buckley and *C. floribundus* (Kük.) R. Carter & S. D. Jones in Appendix 2, because they are commonly weeds of roadsides, poorly kept lawns, pastures, disturbed grasslands, and agricultural

fields; see Carter and Jones (1997) for clarification of the taxonomy of *C. retroflexus* and its allies. *Cyperus floribundus* is native to northeastern Mexico and southern Texas (Carter, in prep.). *Cyperus retroflexus* ranges from northern Mexico north through Texas into Oklahoma and east into western Mississippi, Arkansas, and Missouri and is apparently expanding its range eastward into Alabama, Mississippi, and Missouri (Carter et al., 1987; Carter & Bryson, 1991a, b). *Cyperus plukenetii* also belongs to section *Umbellati*. It has spikelet modifications facilitating animal dispersal (Carter, 1993) and is endemic to the eastern U.S.A., where it is well adapted to open xeric sands of the Coastal Plain (Carter, 1984, in prep.). *Cyperus plukenetii* currently does not appear to be invasive in its natural range; however, because of its specialized dispersal mechanism and adaptation to dry soils, it could potentially become an invasive weed if introduced into suitable habitat elsewhere.

Cyperus aggregatus is frequently cited as a weed (Appendix 2) and has been classified in section *Umbellati* (Kükenthal, 1935–1936). The species was previously called *C. flavus* (Vahl) Nees, nom. illeg., non J. Presl & C. Presl and *C. cayennensis* (Lam.) Britton, non. illeg., non Willd. ex Link (Tucker, 1985). *Cyperus aggregatus* is native to Central and South America, was introduced with ballast in the U.S.A. (Britton, 1886; Mohr, 1901; Horvat, 1941; Tucker et al., 2002), and is also introduced and weedy in Australia (Wilson, 1993). *Cyperus aggregatus* occurs sporadically in the Coastal Plain of the southeastern U.S.A., where it can be locally abundant and somewhat invasive on open, disturbed sandy soils (Bryson & Carter, 1992; Tucker et al., 2002; Carter, pers. obs.). It is likely to continue to expand its range in warmer parts of the southeastern U.S.A. and elsewhere.

Cyperus ligularis L. is occasionally cited as a weed (Appendix 2). It is widely distributed in the West Indies, Mexico, Central America, and South America and is introduced in Africa and the southeastern U.S.A. (O'Neill, 1946; Tucker et al., 2002). It is a frequent weed of disturbed sites in southern peninsular Florida, U.S.A. (Wunderlin, 1998), and Mohr (1901) reported that it was collected in 1891 on ballast at Mobile, Alabama, U.S.A., where it has apparently not survived. Thus, *C. ligularis* is apparently not tolerant of prolonged cold temperatures. *Cyperus ligularis* is readily identified by its robust caespitose habit; coarse lacerating leaves; grayish green foliage; umbelliform inflorescence of dense, oblong-cylindric, often branched spikes; and reddish brown floral scales.

A number of *Cyperus* species colonize coastal or inland sand dunes by forming extensive rhizomes. *Cyperus dentatus* Torr., *C. lecontei* Torr. ex Steud., and *C. onerosus* M. C. Johnst. are related North American species sharing similar growth forms and habitats, spreading vegetatively through growth of rhizomes. *Cyperus lecontei* is listed as a weed by the WSSA (1989), and we have observed it colonizing disturbed sandy roadsides and other open sandy areas along the Gulf Coast. *Cyperus lecontei* and *C. dentatus* are coastal fringe species. *Cyperus lecontei* is found on exposed sands of coastal dunes and swales in the southeastern U.S.A., and *C. dentatus* occupies similar habitats but with a more northerly distribution from the mid-Atlantic states north into the maritime provinces of Canada (Tucker et al., 2002). *Cyperus onerosus* is a related species endemic to swales and pools far inland in nonmaritime dune formations in western Texas (Carter, pers. obs.; Tucker et al., 2002). Rhizomes of *C. dentatus* form tubers, but do not in *C. lecontei* and *C. onerosus* (Tucker et al., 2002). *Cyperus arenarius* Retz. ranges from southern Iran through Pakistan, India, and Ceylon into Indochina (Kükenthal, 1935–1936; Koyama, 1985) and has been introduced into southern Australia and southern Africa (Kukkonen, 2001). Simpson and Inglis (2001) listed it as a weed, and Koyama (1985: 209) described it as a coastal species in Ceylon commenting that its "extensive rhizome system … forms a large pure community." The endemic *C. crassipes* Vahl from coastal southeastern Africa has a similar habit and habitat: sandy seashores and riverbanks (Gordon-Gray, 1995). *Cyperus stoloniferus* Retz., another vegetative colonizer of coastal sands, ranges from Pakistan and India to China and northern Australia and is also known from Mauritius and Madagascar (Kukkonen, 2001). Although only *C. arenarius* and *C. lecontei* are listed in Appendix 2, we think these ecologically similar species have great potential to invade coastal dunes or other open sandy areas, if introduced outside their natural ranges, as the alien *Carex kobomugi* has done along the mid-Atlantic coast of North America (Standley, 1983).

Cyperus fuscus is native to Eurasia and the Mediterranean region of northern Africa and has spread in Asia and Africa and into Greenland, Iceland (Kükenthal, 1935–1936; DeFilipps, 1980c), and North America (Smith, 1867; Britton, 1886; Knowllton et al., 1911; McGivney, 1938; McKenzie et al., 1998). This small caespitose annual produces large numbers of tiny achenes. It is reported as a weed in rice-producing areas of Asia and Portugal and is a common weed in Afghanistan and Israel (Weedon & Stephens, 1969; Holm et al., 1977; Zhirong et al., 1990). Early records of *C. fuscus* in North America were mostly associated with ballast waste and wharf areas (Britton, 1886; Rhoads & Klein, 1993). *Cyperus fuscus* seems to be expanding its range in the U.S.A. (McKenzie et al., 1998), where it is possibly still in the lag phase and could pose problems in the future for rice agriculture.

Cyperus amabilis Vahl, *C. cuspidatus* Kunth, and *C. squarrosus* L. are widely distributed in tropical, subtropical, and warm temperate regions of both the Eastern and Western hemispheres (Kükenthal, 1935–1936; Kern, 1974). All three are diminutive sedges listed in Appendix 2, and both *C. amabilis* and *C. cuspidatus* have prominently cuspidate floral scales. *Cyperus amabilis* has been reported as a weed (Healy & Edgar, 1980; Kühn, 1982) and is known from Africa, Asia, South America, Central America, and North America (Kükenthal, 1935–1936; Tucker et al., 2002). As shown in Appendix 2, *C. cuspidatus* and *C. squarrosus* are listed as weeds of rice and are also found in waste places, disturbed sites, sandy fields, and grasslands. In warmer parts of the southeastern U.S.A., *C. cuspidatus* is sometimes locally abundant in disturbed sandy soils in and around agricultural fields and has also been observed as a weed in container-grown plants and plant nurseries (Carter, pers. obs.). *Cyperus squarrosus* is characterized by the distinctive aroma of fenugreek (*Trigonella foenum-graecum* L.), which is shared by *C. fuscus*, *C. hyalinus* Vahl, and *C. setigerus* Torr. & Hook. (McKenzie et al., 1998; Carter & Mears, 2000). Kern (1974) showed that *C. aristatus* Rottb. is a synonym of *C. squarrosus*, and, subsequently, contemporary workers have followed Kern without reviewing the status of a number of varieties and forms of *C. aristatus* recognized by Kükenthal (1935–1936). North American plants have been segregated as *C. inflexus* Muhl. or *C. aristatus* var. *inflexus* (Muhl.) Boeckeler. Preliminary research (Carter, unpubl. data) indicates that *C. inflexus* is a smaller plant with smaller spikelets and scales and supports its recognition as a distinct endemic North American taxon. The names *C. inflexus* and *C. squarrosus* var. *runyonii* (O'Neill) S. D. Jones & Wipff were placed into synonymy, without justification, under *C. squarrosus* by Tucker et al. (2002). *Cyperus granitophilus* McVaugh is an autotetraploid derivative of *C. squarrosus*, endemic to granite and sandstone outcrops in the Piedmont region from Virginia to Georgia, U.S.A. (Garoni & Murdy, 1964; Tucker et al., 2002). Preliminary observations (Carter, unpubl. data) indicate that *C. granitophilus* is a coarser plant than the more common widespread *C. inflexus* and is morphologically more similar to *C. squarrosus*. Although new taxa have been described and other major nomenclatural changes have occurred, the entire complex has not been studied since Kükenthal (1935–1936). A systematic review worldwide of *C. squarrosus* and related taxa is needed to achieve a consistent treatment of these and other infraspecific taxa not accounted for by contemporary authors.

Cyperus gracilis R. Br., yet another diminutive sedge cited as a weed (Holm et al., 1979), is native to Australia, where it grows in open woodlands and grasslands in drier sites than related species (Wilson, 1993). It was once promoted for use as a ground cover in Hawaii, where it is naturalized and common in disturbed sites, lawns, and roadsides (Hughes, 1995). It is also introduced in California, U.S.A. (Tucker et al., 2002).

Cyperus subg. *Pycreus* is characterized by persistent rachillae, bifid styles, and lenticular achenes with the achene angle adjacent to the rachilla (Kükenthal, 1935–1936; Tucker et al., 2002), which some treat as genus *Pycreus* (e.g., Koyama, 1985; Adams, 1994; Gordon-Gray, 1995). Weeds belonging to subgenus *Pycreus* include *C. flavescens* L., *C. flavicomus* Michx., *C. flavidus* Retz., *C. lanceolatus* Poir., *C. polystachyos* Rottb., *C. puncticulatus* Vahl, *C. pumilus* L., *C. sanguinolentus*, and *C. substramineus* Kük.

Cyperus sanguinolentus has been frequently cited as a weed (Holm et al., 1977; Reed, 1977; Kühn, 1982; Zhirong et al., 1990). It is widely distributed in the Eastern Hemisphere, where it is known from northeastern Africa, the Middle East,

India, Sri Lanka, central Asia, southeastern Asia, China, Taiwan, Japan, Korea, the Philippines, Indonesia, Malaysia, and Australia (Clarke, 1894; Kükenthal, 1935–1936; Ohwi, 1965; Kern, 1974; Holm et al., 1977; Reed, 1977; Kühn, 1982; Haines & Lye, 1983; Zhirong et al., 1990; Wilson, 1993). In the Western Hemisphere, it has been reported from Hawaii (Wagner et al., 1990) and from the Coastal Plain of the southeastern U.S.A. in North America (Carter & Bryson, 2000b, 2001). *Cyperus sanguinolentus* is a weed in paddy and damp, low-dryland crop fields in Asia (Holm et al., 1977; Zhirong et al., 1990). In the southeastern U.S.A. it is a locally common annual weed in periodically disturbed sites with hydric soils, e.g., road ditches and margins of artificial ponds (Carter & Bryson, 2000b). Its introduction into the southeastern U.S.A. is associated with the cultivation of rice, and its dispersal and range expansion there are associated with road construction and maintenance activities (Carter & Bryson, 2000b). *Cyperus louisianensis* Thieret, once thought to be a rare endemic species in southern Louisiana, U.S.A. (Thieret, 1977), has been shown to be the nonindigenous weed *C. sanguinolentus* (Carter & Bryson, 2000b).

Cyperus flavescens is widely distributed in both Old and New Worlds (Kükenthal, 1935–1936; O'Neill, 1946; Barros, 1960; Haines & Lye, 1983; Tucker et al., 2002). It is a common weed of seeps, roadside ditches, and disturbed wet sites in Natal Province (now KwaZulu-Natal Province), South Africa (Gordon-Gray, 1995). In the U.S.A. it is a common tuft-forming weed in drainage ditches, disturbed hydric sites, and moist lawns and fields (Carter, pers. obs.), ranging widely from Florida north into southern Canada and west to Texas and Missouri (Tucker et al., 2002). *Cyperus lanceolatus* is similar to *C. flavescens* and frequently occurs in the same habitats in the southeastern U.S.A. Both taxa have similar habits (dense tufts) and differ primarily in the color of their achenes: black in *C. flavescens*, brown in *C. lanceolatus*. Apparently less tolerant of cold winter temperatures, *C. lanceolatus* is restricted to the warmest parts of the southeastern U.S.A., ranging from Florida north into southern Georgia then west along the coast to Texas (Bryson et al., 1996; Tucker et al., 2002). *Cyperus lanceolatus* also occurs in the West Indies, Mexico, Central and South America, and Africa (O'Neill, 1946; Barros, 1960; Haines & Lye, 1983; Tucker, 1994). Although the type locality is Georgia, U.S.A. (Elliott, 1821), *C. fasciculatus* Elliott is not cited by contemporary American authors (e.g., Tucker, 1994; Tucker et al., 2002) but is cited as a weed in Asia (Appendix 2). This problem should be researched to determine how the name *C. fasciculatus* impinges on nomenclature of the North American plants currently known as *C. flavescens* and *C. lanceolatus*.

Cyperus polystachyos is a cosmopolitan weed, widely distributed in tropical, subtropical, and warm temperate areas (Uittien, 1932; Kükenthal, 1935–1936; Barros, 1960; Kern, 1974; DeFilipps, 1980c; Haines & Lye, 1983; Tucker, 1983, 1994; Koyama, 1985; Wilson, 1993; Adams, 1994; Gordon-Gray, 1995). *Cyperus polystachyos* is cited as a weed of hydric soils in ditches, waste places, grasslands, and disturbed agricultural areas and fields, including rice fields (Kern, 1974; Haines & Lye, 1983). *Cyperus polystachyos* is taxonomically and nomenclaturally complex. Kükenthal (1935–1936) segregated 16 infraspecific taxa from *C. polystachyos* (11 varieties, 5 forms). Also, the relationships between *C. polystachyos* and related taxa like the North American species *C. filicinus* Vahl and *C. fugax* Liebm. are poorly understood and are in need of clarification. We have observed at least three entities passing as *C. polystachyos* in the southeastern U.S.A., with the greatest diversity centered along the Gulf Coast. This group is in need of critical taxonomic review on a worldwide basis. *Cyperus polystachyos* is cited as a weed of hydric soils in ditches, waste places, grasslands, and disturbed agricultural areas and fields, including rice fields (Kern, 1974; Haines & Lye, 1983).

Cyperus flavicomus is found in North America, South America, and Africa (Kükenthal, 1935–1936; Barros, 1960; Tucker, 1994) and in Appendix 2 is cited as a weed of waste places, rice fields and various other crops, pastures, and turf. *Cyperus flavicomus* occurs sporadically on moist soil in and around agricultural fields in the southeastern U.S.A., where it is of minor importance as a weed. *Cyperus pumilus* is a diminutive, densely tufted annual and a minor weed of disturbed sandy soils of rice fields and fallow fields (Kern, 1974; Haines & Lye, 1983; Carter, pers. obs.). As shown in Appendix 2 it is widespread in the Old World. In the New World, *C. pumilus* is known from the West Indies and the U.S.A.

(Kükenthal, 1935–1936; Kern, 1974; Haines & Lye, 1983; Koyama, 1985; Gordon-Gray, 1995). In the U.S.A., *C. pumilus* has long been known from Florida (Chapman, 1889 [as *C. divergens* Kunth]; Small, 1933; Long & Lakela, 1971; Godfrey & Wooten, 1979; Clewell, 1985; Wunderlin, 1998) and was reported in 1996 in southern Georgia (Bryson et al., 1996). *Cyperus pumilus* appears to be spreading in the southeastern U.S.A., as plants were found in northern Georgia in 2003 (*M. Czarnota s.n.*, 29 January 2003, VSC).

Cyperus hyalinus is transitional between *Cyperus* and *Kyllinga* and is pragmatically treated here in subgenus *Queenslandiella* (Domin) Govind. Its taxonomic affinities are unclear, and it has been variously placed in *Pycreus*, *Kyllinga*, *Cyperus*, and the monotypic genus *Queenslandiella* based on morphological traits (Clarke, 1884; Kükenthal, 1935–1936; Kern, 1974; Govindarajalu, 1975; Haines & Lye, 1983). However, recent molecular evidence suggests that *Kyllinga*, *Pycreus*, and, by extension, *Queenslandiella* should be included in *Cyperus* (Muasya et al., 2002). *Cyperus hyalinus* is known from eastern Africa, Madagascar, Mauritius, India, Sri Lanka, tropical Australia (Queensland), and Malaysia (Kükenthal, 1935–1936; Kern, 1974; Haines & Lye, 1983; Koyama, 1985) and has recently been found in southern Florida, where it was apparently introduced by air traffic (Carter & Mears, 2000). Because Haines and Lye (1983: 293) described it as "a weed of sandy soils, near sea level" in eastern Africa and it is similar in habit and habitat to certain weeds in *Kyllinga*, we suspect that *C. hyalinus* could become a pest in turf, flowerbeds, and containerized nursery plants in the southeastern U.S.A. Additional research is needed to determine its potential as a weed and to clarify its taxonomic relationships.

Cyperus laevigatus L. and *C. serotinus* Rottb. are frequently cited as weeds (Appendix 2). Both species have lenticular achenes with the achene face adjacent to the rachilla and, thus, are classified into subgenus *Juncellus*. *Cyperus laevigatus* is cosmopolitan in tropical and warm temperate regions (Kükenthal, 1935–1936; DeFilipps, 1980c). Aquatic biotypes have been reported by Kühn (1982), and this highly variable perennial sedge generally grows in saline, alkaline, or mineral soils associated with salt marshes in coastal areas or salt lakes, hot springs, or artesian wells or along rivers inland (Kükenthal, 1935–1936; Haines & Lye, 1983; Wilson, 1993; Gordon-Gray, 1995; Tucker et al., 2002). *Cyperus laevigatus* was collected along the coast of North Carolina, U.S.A., where it was reportedly introduced with ballast, but it apparently no longer exists there (Radford et al., 1968). A number of varieties were recognized by Kükenthal (1935–1936), which contemporary authors ignore. Wilson (1993) noted the presence of three forms of *C. laevigatus* in Australia and stated the need for its taxonomic study on a worldwide basis. *Cyperus serotinus* occurs from the Mediterranean region of southern Europe through much of Eurasia (Kükenthal, 1935–1936; DeFilipps, 1980c), and it is introduced sparingly in salt marshes along the mid-Atlantic coast of North America (Tucker et al., 2002). Kühn (1982) reported aquatic biotypes in *C. serotinus*, indicating it as a weed of rice fields in Asia. If introduced more widely, *C. serotinus* could pose problems for rice agriculture in North America and elsewhere.

ELEOCHARIS

Eleocharis is a genus of ca. 200 species worldwide (Smith et al., 2002), about half of which are aquatic or semi-aquatic (Holm et al., 1997). Appendix 2 lists 53 species of *Eleocharis* as weeds. Of 118 species of *Eleocharis* studied by Ueno et al. (1989), all but six were shown to have C_3 photosynthesis. Holm et al. (1997) considered *E. acicularis* (L.) Roem. & Schult., *E. dulcis* Trin. ex Hensch., and *E. palustris* (L.) Roem. & Schult. to be among the world's worst weeds and cite *E. acicularis* among the five most troublesome weeds in Asian rice paddies. Elliott (1821: 79) described *E. quadrangulata* (*Scirpus quadrangulatus* Michx.) as "very injurious" in rice fields of Georgia and South Carolina, U.S.A. The tubers of *E. dulcis* are consumed as Chinese water chestnuts, and the species is widely cultivated in Asia (Kern, 1974; Mabberley, 1997). Sculthorpe (1967) cited *E. acicularis* and *E. palustris* among the most broadly distributed aquatic plants in the world, and Svenson (1957) cited the cosmopolitan weed *E. geniculata* (L.) Roem. & Schult. (as *E. caribaea* (Rottb.) S. F. Blake) as the most widespread *Eleocharis* species. As shown in Appendix 2, *E. geniculata* is frequently cited as a weed and has been reported as a pest in rice (Kern, 1974) and taro paddies (Wagner et al., 1990). *Eleocharis radicans*

(Poir.) Kunth is reportedly naturalized in taro paddies in Hawaii (Wagner et al., 1990). Walters (1980) reported the South American species *E. bonariensis* Nees as naturalized on banks of estuarine rivers in France, with no indication of it being a weed.

Eleocharis macrostachya, *E. mamillata* H. Lindb., and *E. palustris* belong to a taxonomically perplexing complex and are widely distributed around the world, found in hydric soils in a variety of habitats, e.g., pond margins, marshes, ditches, and wet meadows (Svenson, 1957; Smith et al., 2002). All three taxa are listed as weeds in Appendix 2. Additionally, the related taxon, *E. erythropoda* Steud., is sometimes associated with disturbance (Smith et al., 2002) and, therefore, might be considered a weed. *Eleocharis palustris* and *E. mamillata* are found in both the Eastern and Western hemispheres, whereas *E. macrostachya* and *E. erythropoda* are restricted to the New World (Smith et al., 2002). *Eleocharis macrostachya* has an essentially western distribution in the U.S.A., ranging from Alaska, south through British Columbia and California, east to Mississippi, Illinois, and Wisconsin; it is also in Mexico and South America (Svenson, 1957; Smith et al., 2002). *Eleocharis macrostachya* seems to be dispersing eastward in the U.S.A. and was only recently reported from western Mississippi where it was locally abundant in hydric soils in a roadside ditch along a major highway (Bryson et al., 1996).

Although none of the primary sources used to compile Appendix 2 lists either *Eleocharis montevidensis* Kunth or *E. montana* (Kunth) Roem. & Schult. as weeds, we have included them based upon observations made in the southeastern U.S.A. *Eleocharis montevidensis* is widely distributed in North and South America and restricted to the Western Hemisphere (Svenson, 1957; Smith et al., 2002). In the southeastern U.S.A., this rhizomatous perennial is sometimes locally abundant and weedy in hydric soils of ditches, roadsides, or other disturbed sites (Carter, pers. obs.). *Eleocharis montana* is a perennial restricted to the Western Hemisphere. It is probably indigenous to South America and is known from the Gulf coastal states of the southern U.S.A., the Caribbean, and throughout much of South America (Svenson, 1957; Smith et al., 2002). In the southeastern U.S.A., *E. montana* is a weed of hydric soils in disturbed areas and roadside ditches and seems to be most common on fine-textured soils in the rice-growing areas of southern Louisiana and eastern Texas (Carter, pers. obs.).

Eleocharis albida is common along the Gulf and Atlantic coasts in the southeastern U.S.A.; it also occurs in Mexico and the Caribbean (Smith et al., 2002). It is often locally abundant in hydric brackish soils of disturbed open sites and ditches adjacent to salt marshes (Carter, 2005). Extensive coastal real estate development has undoubtedly facilitated the expansion of *E. albida* in the southeastern U.S.A. Although we include it in Appendix 2 because of its propensity to form extensive stands following disturbance, we do this with some reservation, because it is indigenous and is apparently invasive only in areas where humans have severely altered the habitat. *Eleocharis parvula* is frequently associated with *E. albida* along the coast in the southeastern U.S.A. (Carter, 2005); however, it is much more widely distributed, ranging throughout much of eastern North America from eastern Canada southward into Central America; it also occurs along the West Coast of North America and in Eurasia (Smith et al., 2002). Like *E. albida*, *E. parvula* can be locally abundant in disturbed, hydric, brackish soils in coastal areas; however, *E. parvula* also occurs sporadically inland. A number of salt marsh species, including the sedges *E. parvula* and *Bolboschoenus robustus* [= *Scirpus robustus* Pursh], occur 400 km from the coast in western Virginia, U.S.A., on saline soils formed by the pumping of brine wells and are thought to have been dispersed there by birds (Sauer, 1988).

Eleocharis baldwinii and *E. vivipara* are listed as weeds (WSSA, 1989). Both species are profuse in their vegetative proliferation and also reproduce from achenes. *Eleocharis baldwinii* is common in parts of the southeastern U.S.A., where it may be locally abundant in dense mats on disturbed moist sandy or peaty soils or floating in ponds or ditches (Carter, pers. obs.). *Eleocharis vivipara* spreads vegetatively, forming dense clumps on moist soil or tangled mats in ponds and ditches (Carter, pers. obs.). In the U.S.A., both *E. baldwinii* and *E. vivipara* are currently of minor economic importance as weeds and are probably only opportunistically weeds following disturbance by humans. However, because of their ability to proliferate vegetatively and to reproduce sexually from achenes, we suspect they could become invasive if introduced into suitable habitats outside their natural ranges.

Eleocharis ovata (Roth) Roem. & Schult. and *E. obtusa* (Willd.) Schult. are cited as weeds (Appendix 2; WSSA, 1989; Callahan et al., 1995) in North America. *Eleocharis ovata* ranges broadly in Eurasia and throughout much of Canada and the northern U.S.A. (Svenson, 1957). *Eleocharis obtusa* is common throughout much of North America and is naturalized in Hawaii (Svenson, 1957; Smith, 2002c) and in rice fields in southern Europe (Walters, 1980). Both *E. ovata* and *E. obtusa* are closely related caespitose annuals (rarely perennials), found in seasonally wet disturbed sites, margins of ponds, and ditches (Svenson, 1957). Tufts of these plants continue to increase in diameter, producing new fertile culms throughout the growing season so long as there is sufficient moisture (Bryson, pers. obs.). *Eleocharis engelmannii* Steud. and *E. lanceolata* Fernald are related taxa, similar to and easily confused with *E. ovata* and *E. obtusa* in habitat and growth characteristics. *Eleocharis engelmannii* occurs sporadically throughout much of the range of *E. obtusa* and differs from that species primarily in its shorter tubercle. *Eleocharis lanceolata* is found in the south-central U.S.A. and was collected in 1949 in California as a weed in a rice field (Smith, 2002c). Hybrids between *E. lanceolata* and closely related *E. obtusa* are known (e.g., *Carr 13969*, VSC). Its narrower, more cylindrical spikelet, acute scale, and narrower tubercle distinguish *E. lanceolata* from *E. obtusa* (Svenson, 1957; Smith, 2002c). *Eleocharis flavescens* (Poir.) Urb. var. *flavescens* and *E. flavescens* var. *olivacea* (Torr.) Gleason, like their New World relative *E. obtusa*, have become naturalized in rice fields of southern Europe (Walters, 1980).

Eleocharis sect. *Limnochloa* (P. Beauv. ex T. Lestib.) Torr. is a group of robust (for *Eleocharis*) emergent aquatics. These perennial species show considerable variation in the shape of their stems in transverse section, from terete, to triquetrous, to quadrangular (Svenson, 1957). As shown in Appendix 2, a number of species in this group are cited as weeds, including *E. acutangula* (Roxb.) Schult., *E. cellulosa* Torr., *E. dulcis*, *E. interstincta* (Vahl) Roem. & Schult., *E. mutata* (L.) Roem. & Schult., *E. philippinensis* Svenson, and *E. quadrangulata*. *Eleocharis acutangula* and *E. mutata* are widely distributed in both hemispheres (Svenson, 1957; Koyama, 1985), whereas *E. cellulosa*, *E. interstincta*, and *E. quadrangulata* are exclusively New World species (Svenson, 1957). *Eleocharis philippinensis* and *E. dulcis* are wide-ranging in the Eastern Hemisphere, where *E. dulcis* is widely introduced and naturalized from cultivation for its tubers (Chinese water chestnuts) (Kern, 1974; Koyama, 1985). Several species are cited as pests in rice fields, and given their aquatic habitat and emergent habit, it would appear that all have the potential to be weeds of rice agriculture or invasive pests of wetlands in natural areas (Kern, 1974; Holm et al., 1979; Koyama, 1985). As discussed in the Dispersal section, there is considerable potential for achenes of these species to be disseminated long distances by waterfowl.

FIMBRISTYLIS

There are more than 100 species of *Fimbristylis* worldwide (Kral, 2002b), and 46 are listed as weeds in Appendix 2. *Fimbristylis dichotoma* (L.) Vahl and *F. miliacea* (L.) Vahl are co-ranked as the world's 40th worst complex of weeds (Holm et al., 1977). *Fimbristylis dichotoma* is a rapidly growing annual or perennial that thrives in poorly aerated soils with high moisture content (Holm et al., 1977). It has been reported as a weed of paddy crops, old rice fields, ditches, lawns, open wetland pastures and meadows, roadsides, cultivated lands, and along forest margins in 21 countries throughout the tropical and semitropical regions of the world including Africa, Asia, the Pacific Islands, and North and South America (Holm et al., 1977). *Fimbristylis dichotoma* is cited as a weed in pineapple, rice, roselle, teak, taro, and other upland row crops (Holm et al., 1977). In the southeastern U.S.A., *F. dichotoma*, *F. caroliniana* (Lam.) Fernald, and *F. castanea* (Michx.) Vahl are frequently weeds following mechanical disturbance of the soil (Kral, 1971).

Fimbristylis miliacea, a native to tropical America, is now a troublesome weed in Africa, Asia, Australia, and North and South America in 21 countries (Holm et al., 1977). It is considered a major weed in rice in Asia, but it is also a weed of taro, bananas, corn, sorghum, and sugarcane (Holm et al., 1977). *Fimbristylis miliacea*, an annual or sometimes perennial in the tropics, is reported to produce more than 1000 seeds per plant per year and without dormancy (Holm et al., 1977). Seeds of *F. miliacea* are easily dispersed and seedlings emerge rapidly on moist soil (Holm et al., 1977). Infestations can constitute 70% of all seedling weeds in agricultural

areas (Verga & Sierra, 1970), and in Malaysia, *F. miliacea* is reported to be the first sedge emerging after rice planting and the first sedge to recover following tillage (Burkill, 1935). Emergence of *F. miliacea* seedlings seems to be environmentally dependent. In Japan, rice planted mid-season reduced the number of emerging *F. miliacea* seedlings by 80% when compared to rice planted early season, and seedling emergence was even less in late-season rice plantings (Noda & Eguchi, 1965).

Fimbristylis annua (All.) Roem. & Schult. and *F. autumnalis* (L.) Roem. & Schult. are also listed as weeds in North America (WSSA, 1989) but are not as troublesome as *F. miliacea* in rice production in the southeastern U.S.A. At least some of the forms of *F. annua* were introduced into the U.S.A. with rice agriculture (Kral, 1971). *Fimbristylis decipiens* Kral was described from specimens collected in the U.S.A. (Kral, 1971). Because it is morphologically similar to and often occurs with *F. annua* and *F. dichotoma*, herbarium specimens of these three species are difficult to distinguish (Kral, 1971). A number of *Fimbristylis* spp. are thought to have been introduced in the U.S.A. and elsewhere around the world with rice agriculture (Appendix 1). *Fimbristylis aestivalis* (Retz.) Vahl has been reported as a weed of rice and in taro paddies in the Eastern Hemisphere and in Hawaii (Kern, 1974; Wagner et al., 1990; Ravi & Mohanan, 2002).

FUIRENA

The 30 species of *Fuirena* worldwide are nearly all heliophytic wetland plants of acidic soils in the tropics and subtropics (Kral, 1980, 2002a). Eight species are listed in Appendix 2, including two, *F. ciliaris* (L.) Roxb. and *F. umbellata* Rottb., cited as weeds of rice fields in the Eastern Hemisphere. *Fuirena breviseta* (Coville) Coville, *F. pumila* (Torr.) Spreng., *F. scirpoidea* Michx., *F. simplex* Vahl, and *F. squarrosa* Michx. are weeds in the U.S.A. (WSSA, 1989), where they occur in wet soils of pastures or along waterways and roadsides. None of the *Fuirena* spp. is a major weed.

ISOLEPIS

Isolepis contains about 69 species worldwide, predominately found in cool-tropical and temperate regions of Africa and Australia (Smith, 2002d); a single species is listed as a weed in Appendix 2. *Isolepis carinata* [= *Scirpus koilolepis* (Steud.) Gleason] is occasionally a weed on moist bare soils in gardens, row crops, and natural areas, following fire or tillage (Carter et al., 1990; Bryson & Hanks, 2001). It is usually not a particularly troublesome weed in row crops because of its diminutive stature, susceptibility to foliar herbicides, and early-season phenology. *Isolepis cernua* is widely distributed around the world primarily in temperate and subtropical regions, occurring in southern Africa (absent from tropical Africa), Eurasia (absent from southeastern Asia), Australia and New Zealand, temperate South America, and North America (Wilson, 1981; Gordon-Gray, 1995; Smith, 2002d). It is apparently a recent arrival (since 1888) in the U.S.A. and Canada, where it is found primarily on the Pacific coast in fresh to brackish water on beaches, dunes, and marine bluffs (Smith, 2002d). It is also known from Texas, where the earliest collection seen by Smith (2002d) was from 1974. The taxonomy of *I. cernua* and related species is in need of revision on a worldwide basis to clarify relationships of taxa and complex nomenclature (Wilson, 1981; Gordon-Gray, 1995). According to Smith (2002d), only *I. cernua* var. *cernua* is known from North America. Although no citations were found of *I. cernua* as a weed, it is included here because of its apparent introduction into the U.S.A. and its potential to be introduced and naturalized elsewhere in temperate and subtropical areas through the ornamental trade (Bailey, 1935; Everett, 1980–1982; Grounds, 1989; Greenlee & Fell, 1992; Huxley, 1992; Darke, 1999).

KYLLINGA

Kyllinga, a genus of short rhizomatous perennials or caespitose annuals, consists of 40 to 45 species distributed in tropical, subtropical, and warm temperate regions around the world (Tucker, 1984, 1987, 2002b). Appendix 2 lists 13 species as weeds, and *K. brevifolia* is among the world's worst weeds, having been reported in 17 crops and 43 countries (Holm et al., 1997). The maximum diversity of *Kyllinga* occurs in tropical East Africa and Madagascar, where there are 30 to 35 species (Kükenthal, 1935–1936; Haines & Lye, 1983). An additional 11 to 12 *Kyllinga* species occur in Asia and two occur in Australia; none is native to Europe and only one is thought to be native to North America. *Kyllinga brevifolia*, *K. gracillima*, *K. odorata* Vahl, *K. pumila* Michx., and *K. squamula-*

ta are known from the continental U.S.A. (Kartesz, 1994). *Kyllinga brevifolia* and *K. nemoralis* (J. R. Forst. & G. Forst.) Dandy ex Hutch. & Dalziel are introduced weeds in Hawaii (Delahoussaye & Thieret, 1967; Holm et al., 1979; Tucker, 1987). *Kyllinga polyphylla* Willd. ex Kunth, a native of Africa, is introduced into Samoa, Tahiti, and Fiji, where it is a weed of disturbed places, pastures, and roadsides at elevations up to 700 m (Whistler, 1994). Spreading by rhizomes, it is a particularly serious pest in pastures because it displaces acceptable forage and is not eaten by livestock (Whistler, 1994).

Kyllinga pumila, a weed of lawns and turf, was initially described in the first North American flora by Michaux (1803) and is evidently the only *Kyllinga* species native to the continental U.S.A. *Kyllinga brevifolia*, *K. gracillima*, *K. odorata*, and *K. squamulata* are all pantropical species (Reed, 1977; Holm et al., 1979; Tucker, 1984, 1987; Koyama, 1985) and were apparently all introduced into the continental U.S.A. from Asia. Although the precise time of their introductions is unknown, *K. brevifolia* was established in the U.S.A. prior to 1821 (Elliott, 1821), and *K. odorata* before 1836 (Torrey, 1836). Both are widespread in the eastern U.S.A., especially in the southern Atlantic and Gulf coastal plains, and are introduced weeds of South America (Bryson et al., 1996; Kissmann, 1997). In the U.S.A., distributions and recent range expansions indicate later introductions for *K. gracillima* and *K. squamulata* (Delahoussaye & Thieret, 1967; Sipple, 1978; Ferren & Schuyler, 1980; Kral, 1981; Webb & Dennis, 1981; Webb et al., 1981; Wunderlin, 1982; Snyder, 1983, 1984; Naczi, 1984; Naczi et al., 1986; Sundell & Thomas, 1988; Bryson & Carter, 1992, 1994; Mears & Libby, 1995; Bryson et al., 1996). *Kyllinga brevifolia* and *K. odorata* have continued to spread northward and westward in the U.S.A., especially as weeds of turf, pastures, and roadways (Bryson & Carter, 1992, 1994; Jones et al., 1993; Bryson et al., 1996), while *K. gracillima* continues to spread south and westward (Sipple, 1978; Ferren & Schuyler, 1980; Kral, 1981; Webb & Dennis, 1981; Webb et al., 1981; Snyder, 1983, 1984; Naczi, 1984; Naczi et al., 1986; Sundell & Thomas, 1988; Bryson & Carter, 1994; Mears & Libby, 1995; Bryson et al., 1996, 1997).

The small achenes of the introduced *Kyllinga* spp. could have arrived in the U.S.A. by a variety of dispersal methods. Following introduction, *Kyllinga* probably first naturalized along sandbars and disturbed areas along streams or in open ruderal sites with adequate moisture. *Kyllinga* spp. are common weeds of highly maintained, frequently irrigated turf in urban areas and on golf courses, and such sites now provide excellent habitat for local proliferation, dispersal, and range expansion of populations (Yelverton, 1996). *Kyllinga* spp. are also frequent weeds of mulched irrigated flowerbeds and containerized nursery plants (Whitwell & Smith, 1997).

Kyllinga brevifolia and *K. gracillima* are rhizomatous perennials, and *K. odorata*, *K. pumila*, and *K. squamulata* are annuals or short-lived perennials in warmer climates. *Kyllinga brevifolia* flowers 10 to 12 weeks after germination and produces mature seeds three weeks after flowering (Holm et al., 1997). *Kyllinga brevifolia* seeds are disseminated by wind and water and germinate without aging (Sumaryono & Basuki, 1986), and human activities result in the movement of whole plants, fragments, or seeds in sod, soil, or grass clippings. A combination of frequent (often daily) irrigation and mowing (3–6 times/week) without removal of clippings, especially around golf course greens, enhances vegetative growth of perennial *Kyllinga* species (Yelverton, 1996). *Kyllinga brevifolia* and *K. gracillima* produce culms that produce fruit below most turfgrass mowing heights (< 1.25 cm), resulting in a reproductive advantage over many other weeds, and they spread rapidly in turf via rhizome growth (Yelverton, 1996). Factors contributing to the increasing importance of *Kyllinga* species as weeds include irrigation of turf, type and timing of herbicide applications, use of fertilizer, and the expansion in the container nursery plants and turfgrass industry to meet the increasing demand for "instant," well-manicured flowerbeds, lawns, and golf courses (Yelverton, 1996; Bryson et al., 1997).

Kyllinga brevifolia and *K. gracillima* are similar in appearance and difficult, if not impossible, to distinguish vegetatively (Yelverton, 1996). Collections of fruiting specimens of *K. gracillima* are primarily from late August until frost, suggesting that the initiation of flowering is dependent upon photoperiod. The more northern distribution of *K. gracillima* in the U.S.A. suggests that it can withstand cooler winter temperatures. *Kyllinga brevifolia*, *K. odorata*, *K. pumila*, and *K. squamulata* flower and produce fruit during the frost-free months throughout their ranges in the continental U.S.A. (Bryson et al., 1997).

LEPIDOSPERMA

Lepidosperma is a genus of ca. 60 species distributed in tropical and subtropical areas of China, Malaysia, Australia, New Caledonia, and New Zealand (Kern, 1974; Mabberley, 1997). One species, *L. chinense* Nees & Meyen, grows in rice fields in southern China (Kern, 1974) and is cited as a weed in Appendix 2.

LEPIRONIA

Lepironia Rich. is a genus of five species distributed in Polynesia and Madagascar (Mabberley, 1997). *Lepironia articulata* (Retz.) Domin, cultivated for fibers used in sails and as packing material (Mabberley, 1997), is a weed of rice fields in Malaysia (Moody, 1989) and is cited in Appendix 2.

LIPOCARPHA

Lipocarpha R. Br. (including *Hemicarpha* Nees) consists of ca. 35 species of wet pantropical and warm temperate regions (Tucker, 2002c). In Appendix 2, three species are cited as weeds of rice or other wet agricultural fields: *Lipocarpha chinensis* (Osbeck) J. Kern, *L. microcephala* (R. Br.) Kunth, and *L. squarrosa* (L.) Goetgh. (Lin, 1968; Kern, 1974; Holm et al., 1979; Kühn, 1982; Koyama, 1985). Additionally, we have observed *L. maculata* (Michx.) Torr. in the southeastern U.S.A. as a weed of disturbed hydric soils, poorly kept moist lawns, roadsides, and ditches. Based upon our observations of its habitat and the citation of congeners as weeds in the Eastern Hemisphere (Kern, 1974; Koyama, 1985), we suspect that *L. maculata* could become a weed in rice fields in the U.S.A. and elsewhere.

MAPANIA

Mapania (including *Thoracostachyum* Kurz) is a genus of 73 species distributed in tropical and subtropical areas of Asia (Mabberley, 1997). *Mapania cuspidata* (Miq.) Uittien grows in rice fields in Indonesia (Moody, 1989) and is cited as a weed in Appendix 2.

OXYCARYUM

Oxycaryum Nees is a monotypic genus widely distributed in the tropics and subtropics of Africa and the Americas (Bruhl, 2002). The only species, *O. cubense*, is in the West Indies (Kunth, 1837), South and Central America (Nees von Esenbeck, 1842; Adams, 1994), the southeastern U.S.A. (Chapman, 1889; Small, 1933; Godfrey & Wooten, 1979; Tucker, 1987), and tropical Africa (Lye, 1971; Hooper & Napper, 1972; Haines & Lye, 1983). In the southeastern U.S.A., it occurs sporadically in Florida (Chapman, 1889; Clewell, 1985; Wunderlin, 1998), southern Georgia (Bryson et al., 1996), southern Alabama (Mohr, 1901; Lelong, 1988), Louisiana (Thomas & Allen, 1993), and coastal Texas (Correll & Johnston, 1970; Hatch et al., 1990; Jones et al., 1997). *Oxycaryum cubense* has spirally arranged scales and has been treated as *Scirpus cubensis* Poepp. & Kunth (e.g., Correll & Johnston, 1970; Godfrey & Wooten, 1979); however, its habit and embryo resemble *Cyperus* (van der Veken, 1965; Lye, 1971), and its taxonomic placement has been disputed: Cypereae (Lye, 1971) and Scirpeae (Bruhl, 1995). The molecular analysis of Muasya et al. (2002) supports classification of *Oxycaryum* in Cypereae. Two forms differing only in gross inflorescence features occur throughout the range of the species. Plants with umbellate inflorescences are called *O. cubense* f. *cubense*, while those with monocephalous inflorescences are called *O. cubense* f. *paraguayense* (Maury) Pedersen (Barros, 1960; Pedersen, 1995). This aquatic species forms extensive floating rafts in ponds, lakes, ditches, or impounded swamps in the southeastern U.S.A. and elsewhere (Haines & Lye, 1983; Bryson et al., 1996). *Oxycaryum cubense* is one of the most vigorous plants (along with *Salvinia molesta* D. S. Mitch. and *Pistia stratiotes* L.) in forming sudds in African lakes (Holm et al., 1977), thereby impeding navigation. In the southeastern U.S.A., *O. cubense* appears to be invasive, with floating mats covering large areas to the exclusion of other aquatic vegetation (Bryson et al., 1996); however, its sporadic distribution in the U.S.A. suggests low fertility of achenes. Its corky buoyant achenes are adapted to dispersal by moving water, and its mat-forming, floating habit facilitates asexual reproduction and transport of vegetative fragments by moving water (Haines & Lye, 1983). *Oxycaryum cubense* has been in the southeastern U.S.A. for more than a century (Chapman, 1889; Mohr, 1901), and we suspect that it was dispersed into North America from the West Indies or South America by migratory birds or with ballast. In order to understand better its dispersal and potential to

invade wetland habitats, additional research into its reproductive biology is needed to determine the extent to which *O. cubense* reproduces sexually and spreads from achenes.

RHYNCHOSPORA

Rhynchospora is a cosmopolitan genus of more than 250 species, most of which inhabit wet, acidic soils (Kral, 2002e). *Rhynchospora* spp. are of little economic importance as weeds, and 20 species are listed in Appendix 2. Although most *Rhynchospora* spp. considered to be weeds are only secondarily or occasionally so, *R. corymbosa* (L.) Britton, *R. holoschoenoides* (Rich.) Herter, *R. submarginata* Kük., and *R. wightiana* (Nees) Steud. are cited as weeds of rice agriculture in the Eastern Hemisphere (Kern, 1974; Simpson & Inglis, 2001). In the U.S.A., *R. corniculata* (Lam.) A. Gray and *R. globularis* (Chapm.) Small are occasionally weeds (WSSA, 1989) along ground transportation routes but usually do not cause economic losses, and dense stands of the caespitose perennial, *R. corniculata*, along waterways impede flow in canals associated with rice production and can cause unwanted flooding of agricultural fields. Several species related to *R. corniculata* are sometimes locally abundant in roadside ditches in the Coastal Plain of the eastern U.S.A. *Rhynchospora macrostachya* Torr. ex A. Gray and *R. corniculata* are found in hydric soils in a variety of wetland habitats, including roadside ditches and margins of artificial ponds, and both are caespitose perennials of wide distribution in eastern North America (Kral, 2002e). The related species, *R. inundata* Fernald and *R. careyana* Fernald, are emergent rhizomatous perennials that form extensive stands in shallow depressions in the flatwoods, including roadside ditches (Kral, 2002e). Although only *R. corniculata* is listed as a weed, we suspect that *R. careyana*, *R. inundata*, and *R. macrostachya* might be invasive, if introduced into similar habitats outside of their natural ranges. *Rhynchospora caduca* Elliott, of little value as forage for livestock, is sometimes a weed in poorly maintained pastures in the southeastern U.S.A. where it is native (Bryson, pers. obs.) and is recently introduced and spreading rapidly in Hawaii (Wagner et al., 1990; Wagner & Herbst, 1995). *Rhynchospora globularis*, another native of the continental U.S.A., was collected in 1982 as an introduction in Hawaii (Wagner et al., 1990) and also occurs in northern California (Cranfil, 1993) where it is perhaps introduced from the eastern U.S.A. Other *Rhynchospora* spp. that opportunistically spread into artificially disturbed sites within their native ranges in the southeastern U.S.A. include *R. cephalantha* A. Gray, *R. debilis* Gale, *R. fascicularis* (Michx.) Vahl, *R. glomerata* (L.) Vahl, *R. fernaldii* Gale, *R. inexpansa* (Michx.) Vahl, *R. microcephala* (Britton) Britton ex Small, *R. odorata* C. Wright ex Griseb., and *R. torreyana* A. Gray (Godfrey & Wooten, 1979; Bryson & Carter, pers. obs.). We suspect that such plants would likely become invasive if introduced into suitable habitats elsewhere, as *R. caduca* has in Hawaii.

SCHOENOPLECTUS

Schoenoplectus is a genus of 77 species worldwide (Smith, 2002b), of which 20 are cited as weeds in Appendix 2. *Schoenoplectus mucronatus* (L.) Palla [= *Scirpus mucronatus* L.], considered to be among the world's worst weeds (Holm et al., 1997), is a pest in rice and other row and tree crops in Bangladesh, France, India, Malaysia, the Philippines, Portugal, Spain, and the U.S.A. (Holm et al., 1997). *Schoenoplectus mucronatus* is a greater problem in paddy fields where hand labor is the primary method of weed control than in rice production involving mechanical tillage and the use of herbicides. *Schoenoplectus grossus* (L. f.) Palla [= *Scirpus grossus* L. f.] is a weed of rice, riverbeds, reservoirs, and irrigation systems in southeastern Asia including regions of Vietnam, India, and the Philippines, and *S. tabernaemontani* is also listed as a weed of rice in China (Zhirong et al., 1990). *Schoenoplectus juncoides* (Roxb.) Palla is reportedly naturalized in rice fields in Europe (DeFilipps, 1980a). *Schoenoplectus acutus* and *S. americanus* (Pers.) Volkart ex Schinz & R. Keller are weeds in wetland areas of North America (WSSA, 1989; Callahan et al., 1995), while *S. californicus* (C. A. Mey.) Soják is reported as a weed in North America and Brazil (WSSA, 1989; Kissmann, 1997).

SCIRPODENDRON

Scirpodendron Zipp. ex Kurz is a genus of two species ranging from Sri Lanka and southeastern Asia through Malesia to Australia and Polynesia (Goetghebeur, 1998). *Scirpodendron* inhabits fresh-

water tidal swamps, tidal swamp forests, and forests adjacent to mangroves, and its large fruits are dispersed by water (Kern, 1974). It is cultivated in Sumatra for its leaves, which are used for thatching and weaving mats and hats (Kern, 1974). *Scirpodendron ghaeri* (Gaertn.) Merr. has been cited as a weed of rice fields in Asia (Moody, 1989).

SCIRPUS

Scirpus is a genus of 35 species widely distributed in North America, Mexico, Eurasia, Australia, and the Pacific Islands (Whittemore & Schuyler, 2002). Eight species are listed as weeds in Appendix 2, none of which is invasive in agricultural croplands. *Scirpus atrovirens* Willd., *S. pendulus* Muhl., and *S. cyperinus* (L.) Kunth are native to North America and cited as weeds there (WSSA, 1989; Callahan et al., 1995). These *Scirpus* species are occasional weeds along roadsides and waterways and in wet pastureland but rarely cause economic losses. *Scirpus atrovirens* and *S. pendulus* are naturalized in Europe (DeFilipps, 1980a). In the U.S.A., where it is native, *S. cyperinus* sometimes forms extensive stands dominating disturbed wetlands (Carter, pers. obs.), and we strongly suspect it would be an invasive pest if introduced into suitable habitats outside its natural range.

SCLERIA

Scleria is widely distributed in tropical and subtropical regions around the world and consists of ca. 200 species (Reznicek et al., 2002). As shown in Appendix 2, 24 species are weeds, a number of which are aquatics and known or potential weeds of rice agriculture (e.g., *Scleria biflora* Roxb., *S. laevis* Retz., *S. lithosperma* (L.) Sw., *S. novae-hollandiae* Boeckeler). The non-native invasive weed *S. lacustris* C. Wright has been found in freshwater marshes of peninsular Florida, U.S.A., where it can be locally abundant and dominant in water up to 1 m deep, forming dense stands and displacing native vegetation (Tobe et al., 1998; Wunderlin, 1998; Jacono, 2001). *Scleria lacustris* seems to require recession of standing water in order to become established (Jacono, 2001). It is thought to be native in scattered areas of the Neotropics, Africa, and Madagascar (Core, 1933; Hennessy, 1985) and is known from Brazil, Cuba, Costa Rica, French Guiana, Guyana, Jamaica, Paraguay, Suriname, U.S.A., and six countries across tropical Africa (Jacono, 2001). Additional research is needed to determine the ecological range of *S. lacustris* and control strategies. *Scleria vaginata* Steud. is an aggressive vine native to Central and South America that was collected once in southern Florida, U.S.A. (Reznicek et al., 2002), and we suspect it could be invasive if introduced into tropical and subtropical areas outside its native range.

DISCUSSION

Cyperaceae is a large, diverse, cosmopolitan family, and many of its species are biologically predisposed to spread opportunistically into areas altered by humans. Data compiled in Appendix 1 show that humans have played a tremendous role in the dispersal of sedges, including many weeds. Given the fundamental importance of dispersal and habitat disturbance in the evolution and survival of weeds and their intrinsic attributes favoring competition, colonization, and migration, it is not surprising that many sedges have evolved and continue to evolve as weeds. The magnitude of the human "footprint" on Earth is immense. Given the role that humans play in destruction and conversion of natural areas into disturbed and highly artificial ruderal habitats and urban and agricultural systems, it is axiomatic that the numbers of noxious weeds and invasive plant species will increase in step with the human population.

It is difficult to anticipate which species will become weeds, and where and under what circumstances they will be invasive. *Rhynchospora caduca*, a seemingly innocuous sedge native to the southeastern U.S.A., has recently been reported as an invasive weed in Hawaii (Wagner & Herbst, 1995). *Rhynchospora caduca* is not extraordinary among the beak-rushes in the southeastern U.S.A., which suggests that any number of apparently harmless species could pose similar problems in an alien environment. Insular systems, such as the Hawaiian Islands, have great potential as natural laboratories for the study of invasion.

Appendix 2 is a list of 447 species of Cyperaceae cited as weeds, which was compiled from more than 60 publications. Most cyperaceous weeds are from tropical and subtropical regions, and the most trou-

blesome sedges (*Cyperus rotundus*, *C. esculentus*, *C. difformis*, and *C. iria*) are native to Asia and Africa but are now widely dispersed on other continents.

In order to examine the impact of humans on dispersal and introduction of cyperaceous weeds, we noted commonalities in listings of species in Appendices 1 and 2 and used these data to construct Table 4. Thus, Table 4 shows the number of weed species in each genus that are known or suspected to have been anthropogenically dispersed. When Appendices 1 and 2 are compared, 111 species are common to both lists (Table 4) with the greatest number of cyperaceous weeds known or suspected to be dispersed by humans in *Cyperus* (43 spp., ca. 39%), followed by *Carex* (24 spp., ca. 22%); *Eleocharis* (9 spp., ca. 8%); *Fimbristylis* (8 spp., 7%); *Kyllinga* and *Schoenoplectus* (6 spp. each, 5%); *Scirpus* (5 spp. each, ca. 5%); *Rhynchospora* (3 spp., ca. 3%); *Fuirena* (2 spp., ca. 2%); and *Bolboschoenus, Bulbostylis*, *Lepironia*, *Lipocarpha*, and *Mapania* (1 spp. each, ca. 1%).

Cyperus, by far, has been subject to greater anthropogenic dispersal than the other cyperaceous genera, which undoubtedly has been an important factor. It is readily concluded from Appendix 1 that *Cyperus* spp. have been mostly introduced unintentionally through a variety of human activities, especially as contaminants of seeds (particularly rice), wool, and dumping of ship's ballast. It seems reasonable to conclude from these data that systematic surveys of flora in vicinity of ports of entry are needed for early detection of new introductions and reintroductions and to understand better the dynamics of inadvertent importation of noxious weeds.

The role of rice agriculture in the introduction of cyperaceous weeds has long been recognized and is reinforced by data presented in Appendix 1. The number of cyperaceous weeds associated with rice agriculture in Appendix 2 is great, and, despite advancements in the regulation of importation of grain, there still exists the possibility of unintentional movement and introduction of other potentially noxious sedges as contaminants in shipments of seeds. These data indicate the need for continued vigilance and regulation of movement and importation of sedges throughout the world.

Historically, *Carex* spp. have received little attention as agricultural weeds. However, Kukkonen (2001) includes rice fields in Pakistan as habitats of *Carex diandra*, *C. pycnostachya*, and *C. divisa* Huds., and he describes *C. songorica* Kar. & Kir., *C. diluta* M. Bieb., and *C. orbicularis* Boott as growing in irrigation channels. The latter set of species is not listed in Appendix 2, which includes only entries explicitly characterized as weeds or invasives or directly associated with agricultural fields, gardens, or turf. However, populations of native sedges that have spread into irrigation canals associated with agriculture have certainly adapted to human disturbance, and biotypes adapted to conditions in the adjacent fields could easily evolve.

The large number of ornamental and cultivated sedges (>150 spp.) listed in Appendix 1 was not anticipated. Of particular interest is the increasing horticultural usage of sedges, especially *Carex* spp., as ornamentals (Figs. 2 and 3). This indicates a need for increased research into the reproductive biology, physiology, and growth characteristics of ornamental sedges to determine which species may be safely used and where and which will likely become invasive. There is also a need for greater awareness about problems inherent in the unwise and irresponsible use of ornamental sedges and additional measures toward intervention to prevent the transportation and importation of ornamental sedges.

Because of their distributions across vast latitudinal, altitudinal, and climatic ranges and diverse habitats, populations of widely distributed weeds have been subject to a great array of environmental factors resulting in much localized natural (and artificial) selection and diversification. Thus, in general, the taxonomy of weeds is far more complex than of other plants, which is evident in the complex nomenclature of the most widely distributed weeds, e.g., *Cyperus esculentus*, *C. rotundus* (Haines & Lye, 1983), *C. polystachyos* (cf. Kükenthal, 1935–1936), and *C. sanguinolentus* (cf. Kükenthal, 1935–1936; Kern, 1974). To resolve basic questions about relationships within these taxa, there is a great need for additional morphometric, field-, and herbarium-based research into the variation and taxonomy on a worldwide basis. The increased use of molecular techniques (e.g., Muasya et al., 2000a, b, 2002) should help to stabilize nomenclature by resolving the taxonomic status and rank of certain disputed groups, e.g., the segregates of *Cyperus* and *Scirpus*. In the future, the results of molecular research will elucidate much about the pathways of introduction

Table 4. Numbers and percentages of species of Cyperaceae by genus, which have been cited as weeds and are known or suspected to be dispersed by humans (data extracted from Appendices 1 and 2).[1]

Genus	Species (incl. infrasp.)	Percent of Total
Cyperus[2]	43	39
Carex	24	22
Eleocharis	9	8
Fimbristylis	8	7
Kyllinga	6	5
Schoenoplectus	6	5
Scirpus	5	5
Rhynchospora	3	3
Fuirena	2	1
Bolboschoenus	1	1
Bulbostylis	1	1
Lepironia	1	1
Lipocarpha	1	1
Mapania	1	1
Abildgaardia	0	0
Caustis	0	0
Cladium	0	0
Courtoisina	0	0
Cymophyllus	0	0
Desmoschoenus	0	0
Eriophorum	0	0
Gahnia	0	0
Isolepis	0	0
Kobresia	0	0
Lepidosperma	0	0
Machaerina	0	0
Oreobolus	0	0
Oxycaryum	0	0
Schoenus	0	0
Scleria	0	0
Trichophorum	0	0
Uncinia	0	0
Total	111	~100

[1] Authority names for genera in Table 4 not discussed elsewhere in this paper are as follows: *Caustis* R. Br.; *Desmoschoenus* Hook f.; *Kobresia* Willd.; *Oreobolus* R. Br.; *Schoenus* L.; *Trichophorum* Pers.

[2] Includes *Diclidium*, *Juncellus*, *Mariscus*, *Pycreus*, and *Queenslandiella*.

and migration of invasive weeds. Introduction of new weeds is increasingly a problem because of the frequency and ease of long-distance and international transportation, and advances in basic research will result in molecular assays useful in detecting and stopping weeds at ports of entry and in more accurately diagnosing infestations of herbicide-resistant biotypes of weeds.

Given the economics of weed control, including indirect costs (e.g., increased cost of health care, remediation of environmental damage), every precaution should be taken to avoid tagging indigenous plants as weeds without compelling supportive evidence. Realistically and pragmatically, it is most certainly advantageous and desirable for native plants to occupy roadsides and other artificial habitats than alien weeds. There is a great need for basic research to determine the ecological tolerances and invasive potentials and limits of indigenous and nonindigenous weeds. For only through the results of such research will basic knowledge be advanced sufficiently to allow applied scientists, natural resource managers, and the public to make informed, intelligent decisions about which plants to promote, which to exclude, which to suppress, and when to suppress them.

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APPENDIX 1

Known and suspected anthropogenic dispersal in Cyperaceae.

Species[1]	Method of dispersal	Source
Bolboschoenus glaucus (Lam.) S. G. Sm.	planted as waterfowl food, rice agriculture	Browning et al., 1995; Smith, 2002a
Bolboschoenus maritimus (L.) Palla	rice agriculture	Holm et al., 1997
Bolboschoenus maritimus subsp. *paludosus* (A. Nelson) T. Koyama	planted as waterfowl food	Smith, 2002a
Bolboschoenus robustus (Pursh) Soják	ornamental	Everett, 1980–1982
Bulbostylis humilis (Kunth) C. B. Clarke	wool alien	Sell & Murrell, 1996
Bulbostylis striatella C. B. Clarke	wool alien	Sell & Murrell, 1996
Carex acuta L.	ornamental	Grounds, 1989; Huxley, 1992
Carex acutiformis Ehrh.	ornamental	Huxley, 1992
Carex alba Scop.	ornamental	Huxley, 1992
Carex albula Allan	ornamental	Greenlee & Fell, 1992; Turner & Wasson, 1998; Darke, 1999
Carex appressa R. Br.	erosion control, wool alien	Huxley, 1992; Sell & Murrell, 1996; Simpson & Inglis, 2001
Carex arenaria L.	ornamental	Huxley, 1992
Carex atrata L.	ornamental	Grounds, 1989; Huxley, 1992
Carex austrina Mack.	railroad adventive	Mühlenbach, 1983
Carex baccans Nees	ornamental	Bailey, 1935; Greenlee & Fell, 1992; Huxley, 1992; Darke, 1999
Carex baldensis L.	ornamental	Huxley, 1992
Carex baltzellii Chapm. ex Dewey	ornamental	Darke, 1999
Carex berggreni Petrie	ornamental	Grounds, 1989; Huxley, 1992; Darke, 1999
Carex brevior (Dewey) Mack. ex Lunell	contaminated grass seed	Bryson et al., 1992
Carex brunnea Thunb.	ornamental	Grounds, 1989; Huxley, 1992
Carex buchananii Berggr.	ornamental	Bailey, 1935; Brooklyn Botanical Garden, 1988; Ottesen, 1989; Greenlee & Fell, 1992; Darke, 1999
Carex caryophyllea Latourr.	ornamental	Huxley, 1992; Darke, 1999
Carex cherokeensis Schwein.	hay	Bryson, pers. obs.
Carex comans Berggr.	ornamental	Everett, 1980–1982; Greenlee & Fell, 1992; Turner & Wasson, 1998; Darke, 1999
Carex conica Boott	ornamental	Bailey & Bailey, 1976; Ottesen, 1989; Greenlee & Fell, 1992; Darke, 1999
Carex crawfordii Fernald	railroad adventive	Mühlenbach, 1983
Carex crinita Lam.	ornamental	Darke, 1999
Carex curvula All.	ornamental	Huxley, 1992
Carex devia Cheeseman	wool alien	Sell & Murrell, 1996

Species[1]	Method of dispersal	Source
Carex deweyana Schwein.	wool alien	Sell & Murrell, 1996
Carex diandra Schrank	ornamental	Huxley, 1992
Carex digitata L.	ornamental	Huxley, 1992; Darke, 1999
Carex dipsacea Berggr.	ornamental	Grounds, 1989; Huxley, 1992; Turner & Wasson, 1998
Carex dissita Sol. ex Hook. f.	ornamental	Huxley, 1992
Carex divulsa Stokes subsp. *leersii* (Kneuck.) W. Koch	ornamental	Grounds, 1989
Carex dolichostachya Hayata	ornamental	Darke, 1999
Carex eburnea Boott in Hook.	ornamental	Darke, 1999
Carex elata All.	ornamental	Grounds, 1989; Ottesen, 1989; Greenlee & Fell, 1992; Huxley, 1992; Turner & Wasson, 1998; Darke, 1999
Carex exserta Mack.	revegetation	Ratliff & Westfall, 1992
Carex firma Host	ornamental	Grounds, 1989; Huxley, 1992; Darke, 1999
Carex flacca Schreb.	ornamental	Grounds, 1989; Huxley, 1992; Darke, 1999
Carex flaccosperma Dewey	ornamental	Darke, 1999
Carex flagellifera Colenso	ornamental, wool alien	Sell & Murrell, 1996; Ottesen, 1989; Greenlee & Fell, 1992; Turner & Wasson, 1998
Carex flava L.	ornamental	Ottesen, 1989
Carex gallaecica H. Lév. & Vaniot	ornamental	Bailey, 1935
Carex gaudichaudiana Kük.	ornamental	Bailey, 1935; Huxley, 1992
Carex geyeri Boott	erosion control	Hermann, 1970
Carex grayi J. Carey	ornamental	Bailey & Bailey, 1976; Grounds, 1989; Greenlee & Fell, 1992; Turner & Wasson, 1998; Darke, 1999
Carex hachijoensis Akiyama	ornamental	Grounds, 1989; Greenlee & Fell, 1992; Huxley, 1992; Darke, 1999
Carex hirta L.	ballast	Brown, 1880
Carex hoodii Boott in Hook.	erosion control	Hermann, 1970
Carex hubbardii Nelmes	wool alien	Sell & Murrell, 1996
Carex humilis Leyss.	ornamental	Huxley, 1992
Carex intumescens Rudge	ornamental	Bailey, 1935; Huxley, 1992
Carex inversa R. Br.	wool alien	Sell & Murrell, 1996
Carex kaloides Petrie	ornamental	Huxley, 1992
Carex kobomugi Ohwi	ballast, planted for dune stabilization	Champlin, 1994; Mastrogiuseppe, 2002
Carex longebrachiata Boeckeler	wool alien	Sell & Murrell, 1996
Carex longii Mack.	hay, pine-bark mulch	Bryson, pers. obs.
Carex lupulina Muhl. ex Willd.	ornamental	Darke, 1999
Carex montana L.	ornamental	Huxley, 1992; Darke, 1999

Appendix 1. Continued.

Species[1]	Method of dispersal	Source
Carex morrowii Boott	ornamental	Bailey, 1935; Bailey & Bailey, 1976; Everett, 1980–1982; Grounds, 1989; Ottesen, 1989; Greenlee & Fell, 1992; Huxley, 1992; Turner & Wasson, 1998; Darke, 1999
Carex muskingumensis Schwein.	ornamental	Brooklyn Botanical Garden, 1988; Grounds, 1989; Ottesen, 1989; Greenlee & Fell, 1992; Huxley, 1992; Darke, 1999
Carex nebrascensis Dewey	railroad adventive	Mühlenbach, 1979
Carex nigra (L.) Reichard	ornamental	Ottesen, 1989; Greenlee & Fell, 1992; Huxley, 1992; Darke, 1999
Carex nudata W. Boott in S. Watson	ornamental	Greenlee & Fell, 1992; Turner & Wasson, 1998; Darke, 1999
Carex oklahomensis Mack.	hay, highway construction	Bryson et al., 1992, 1996
Carex ornithopoda Willd.	ornamental	Grounds, 1989; Ottesen, 1989; Greenlee & Fell, 1992; Huxley, 1992; Darke, 1999
Carex oshimensis Nakai	ornamental	Grounds, 1989; Darke, 1999
Carex pallescens L.	ornamental	Darke, 1999
Carex paniculata L.	ornamental	Huxley, 1992; Heywood, 1993
Carex pansa L. H. Bailey	ornamental	Greenlee & Fell, 1992; Darke, 1999
Carex pendula Huds.	ornamental	Bailey & Bailey, 1976; Everett, 1980–1982; Grounds, 1989; Ottesen, 1989; Greenlee & Fell, 1992; Huxley, 1992; Darke, 1999; Reznicek, 2002
Carex pensylvanica Lam.	ornamental	Darke, 1999
Carex petriei Cheeseman	ornamental	Grounds, 1989; Greenlee & Fell, 1992; Huxley, 1992; Darke, 1999
Carex phyllocephala T. Koyama	ornamental	Grounds, 1989; Greenlee & Fell, 1992; Darke, 1999
Carex pilulifera L.	ornamental	Grounds, 1989; Darke, 1999
Carex plantaginea Lam.	ornamental	Bailey & Bailey, 1976; Grounds, 1989; Greenlee & Fell, 1992; Huxley, 1992
Carex praegracilis W. Boott	highway construction and maintenance, ornamental	Reznicek et al., 1976; Bruton & Catling, 1982; Cusick, 1984; Reznicek & Catling, 1987; Darke, 1999
Carex pseudocyperus L.	ornamental	Brooklyn Botanical Garden, 1988; Greenlee & Fell, 1992; Huxley, 1992; Darke, 1999
Carex riparia Curtis	ornamental	Bailey, 1935; Everett, 1980–1982; Grounds, 1989; Huxley, 1992; Darke, 1999
Carex scaposa C. B. Clarke	ornamental	Huxley, 1992
Carex secta Boott	wool alien	Sell & Murrell, 1996
Carex siderosticta Hance	ornamental	Grounds, 1989; Greenlee & Fell, 1992; Huxley, 1992; Darke, 1999
Carex solandri Boott	ornamental, wool alien	Sell & Murrell, 1996; Darke, 1999

Species[1]	Method of dispersal	Source
Carex spectabilis Dewey	erosion control	Hermann, 1970
Carex spissa L. H. Bailey	ornamental	Greenlee & Fell, 1992; Turner & Wasson, 1998; Darke, 1999
Carex stricta Lam.	ornamental	Ottesen, 1989; Darke, 1999
Carex sylvatica Huds.	ornamental	Brooklyn Botanical Garden, 1988; Greenlee & Fell, 1992; Huxley, 1992
Carex temnolepis Franch.	ornamental	Greenlee & Fell, 1992
Carex tereticaulis F. Muell.	wool alien	Sell & Murrell, 1996
Carex testacea Sol. ex Boott	ornamental	Greenlee & Fell, 1992; Turner & Wasson, 1998; Darke, 1999
Carex texensis (Torr.) L. H. Bailey	ornamental	Greenlee & Fell, 1992
Carex trifida Cav.	ornamental	Huxley, 1992
Carex tumulicola Mack.	ornamental	Greenlee & Fell, 1992; Turner & Wasson, 1998; Darke, 1999
Carex umbrosa Host	ornamental	Huxley, 1992
Carex uncifolia Cheeseman	ornamental	Grounds, 1989; Huxley, 1992
Carex uruguensis Boeckeler	erosion control	Pio Corrêa, 1926–1984
Carex vilmorini Mottet	ornamental	Greenlee & Fell, 1992
Carex virgata Boott ex Hook. f.	wool alien	Sell & Murrell, 1996
Carex vulpina L.	ornamental	Huxley, 1992
Carex vulpinoidea Michx.	possibly introduced with fodder or other seed, wool alien	Sell & Murrell, 1996
Caustis dioica R. Br.	ornamental	Simpson & Inglis, 2001
Cymophyllus fraserianus (Ker Gawl.) Kartesz & Gandhi	ornamental	Bailey, 1935; Bailey & Bailey, 1976; Everett, 1980–1982; Grounds, 1989; Huxley, 1992; Turner & Wasson, 1998; Darke, 1999
Cyperus adenophorus Schrad.	ornamental	Everett, 1980–1982
Cyperus aggregatus (Willd.) Endl.	ballast, wool alien	Britton, 1886; Mohr, 1901; Horvat, 1941; Sell & Murrell, 1996; Tucker et al., 2002
Cyperus albostriatus Schrad.	ornamental, naturalized ornamental	Bailey, 1935; Bailey & Bailey, 1976; Everett, 1980–1982; Greenlee & Fell, 1992; Wilson, 1993; Brickell & Zuk, 1997; Turner & Wasson, 1998; Darke, 1999
Cyperus alopecuroides Rottb.	contaminant of nursery stock	Carter et al., 1996
Cyperus alternifolius L. subsp. *flabelliformis* Kük.	garden escape, naturalized ornamental	Bailey, 1935; Kern, 1974; Bailey & Bailey, 1976; Brickell & Zuk, 1997; Everett, 1980–1982; Burkill, 1985; Koyama, 1985; Wagner et al., 1990; Greenlee & Fell, 1992; Huxley, 1992; Sell & Murrell, 1996; Turner & Wasson, 1998; Darke, 1999
Cyperus bulbosus Vahl	ornamental	Simpson & Inglis, 2001
Cyperus capitatus Vand.	erosion control	Simpson & Inglis, 2001
Cyperus chordorrhizus Chiov.	erosion control, revegetation	Simpson & Inglis, 2001

Appendix 1. Continued.

Species[1]	Method of dispersal	Source
Cyperus clarus S. T. Blake	wool alien	Sell & Murrell, 1996
Cyperus compressus L.	ballast, ornamental	Smith, 1867; Britton, 1886; Bailey, 1935; Huxley, 1992; Gordon-Gray, 1995
Cyperus congestus Vahl	ornamental, wool alien	Huxley, 1992; Sell & Murrell, 1996
Cyperus conglomeratus Rottb.	erosion control, ornamental	Bailey, 1935; Burkill, 1985
Cyperus croceus Vahl	ballast, wool alien	Smith, 1867; Britton, 1886; Sell & Murrell, 1996
Cyperus cyperinus (Retz.) Suringar	ornamental, wool alien	Huxley, 1992; Sell & Murrell, 1996
Cyperus dactylotes Benth.	wool alien	Sell & Murrell, 1996
Cyperus difformis L.	rice agriculture	Holm et al., 1977; Lipscomb, 1980; Wagner et al., 1990
Cyperus echinatus (L.) A. W. Wood	wool alien	Sell & Murrell, 1996
Cyperus elegans L.	ornamental	Darke, 1999
Cyperus entrerianus Boeckeler	highway construction and maintenance, rice agriculture	Carter, 1990; Carter & Bryson, 1996
Cyperus eragrostis Lam.	naturalized ornamental, wool and grass-seed alien	Grounds, 1989; Huxley, 1992; Sell & Murrell, 1996; Brickell & Zuk, 1997; Darke, 1999
Cyperus erythrorhizos Muhl.	ornamental	Huxley, 1992
Cyperus esculentus L.	cultivated for tubers, wool alien	Bailey, 1935; Bailey & Bailey, 1976; Holm et al., 1977; Sell & Murrell, 1996; Turner & Wasson, 1998; Darke, 1999; Miller & Miller, 1999
Cyperus fertilis Boeckeler	ornamental	Bailey, 1935; Huxley, 1992
Cyperus filicinus Vahl	ornamental	Huxley, 1992
Cyperus fuscus L.	ballast	Smith, 1867; Britton, 1886
Cyperus giganteus Vahl	water purification	Pio Corrêa, 1926–1984
Cyperus gracilis R. Br.	ground cover	Hughes, 1995
Cyperus gunnii Hook. f.	wool alien	Sell & Murrell, 1996
Cyperus haspan L.	ornamental, rice agriculture	Holm et al., 1997; Everett, 1980–1982; Darke, 1999
Cyperus hyalinus Vahl	air traffic	Carter & Mears, 2000
Cyperus imbricatus Retz.	ballast	McGivney, 1938
Cyperus iria L.	rice agriculture	Holm et al., 1977; Koyama, 1985
Cyperus jeminicus Rottb.	erosion control	Simpson & Inglis, 2001
Cyperus laevigatus L.	ballast	Radford et al., 1968
Cyperus ligularis L.	ballast	Mohr, 1901; Horvat, 1941
Cyperus longus L.	ornamental	Bailey, 1935; Brickell & Zuk, 1997; Darke, 1999
Cyperus lucidus R. Br.	ornamental	Bailey, 1935
Cyperus luzulae (L.) Rottb. ex Retz.	wool alien	Sell & Murrell, 1996
Cyperus natalensis Hochst.	ornamental	Bailey, 1935

Species[1]	Method of dispersal	Source
Cyperus odoratus L.	railroad adventive	Mühlenbach, 1983
Cyperus owanii Boeckeler	naturalized ornamental	Bailey & Bailey, 1976; Huxley, 1992
Cyperus papyrus L.	naturalized ornamental	Bailey, 1935; Bailey & Bailey, 1976; Everett, 1980–1982; Grounds, 1989; Wagner et al., 1990; Greenlee & Fell, 1992; Huxley, 1992; Wilson, 1993; Brickell & Zuk, 1997; Turner & Wasson, 1998; Darke, 1999
Cyperus pilosus Vahl	rice agriculture	McGivney, 1938; Wagner et al., 1990
Cyperus planifolius Rich.	ballast	Horvat, 1941
Cyperus plukenetii Fernald	attachment to clothing	Carter, 1993
Cyperus prolifer Lam.	naturalized ornamental	Bailey & Bailey, 1976; Everett, 1980–1982; Greenlee & Fell, 1992; Huxley, 1992; Carter et al., 1996; Brickell & Zuk, 1997; Darke, 1999
Cyperus pulcher Thunb.	recommended for cultivation in water gardens	Gordon-Gray, 1995
Cyperus reflexus Vahl	wool alien	Sell & Murrell, 1996
Cyperus retroflexus Buckley	ballast?	Horvat, 1941
Cyperus rigidifolius Steud.	wool alien	Sell & Murrell, 1996
Cyperus rotundus L.	agriculture, animals, ballast, machinery, wool alien	Smith, 1867; Britton, 1886; Holm et al., 1977; Sell & Murrell, 1996; Miller & Miller, 1999
Cyperus rutilans (C. B. Clarke) Maiden & Betche	wool alien	Sell & Murrell, 1996
Cyperus sanguinolentus Vahl	highway construction and maintenance, rice agriculture	Carter & Bryson, 2000b
Cyperus sexangularis Nees	water gardens	Gordon-Gray, 1995
Cyperus sphacelatus Rottb.	ballast	Britton, 1886; Mohr, 1901; McGivney, 1938
Cyperus sporobolus R. Br.	wool alien	Sell & Murrell, 1996
Cyperus stoloniferus Retz.	erosion control	Burkill, 1935
Cyperus strigosus L.	ornamental	Bailey, 1935
Cyperus subumbellatus Kük.	ornamental	Simpson & Inglis, 2001
Cyperus surinamensis Rottb.	ballast	Britton, 1886
Cyperus tenuis Sw.	wool alien	Sell & Murrell, 1996
Cyperus textilis Thunb.	cultivated, presumably as an ornamental	Gordon-Gray, 1995
Cyperus umbellatus Benth.	ballast	Brown, 1880
Cyperus ustulatus A. Rich.	wool alien	Sell & Murrell, 1996
Cyperus vaginatus R. Br.	wool alien	Sell & Murrell, 1996
Desmoschoenus spiralis (A. Rich.) Hook. f.	ornamental	Grounds, 1989
Eleocharis acicularis (L.) Roem. & Schult.	rice agriculture, ornamental	Bailey, 1935; Bailey & Bailey, 1976; Everett, 1980–1982; Holm et al., 1997; Turner & Wasson, 1998; Darke, 1999

Appendix 1. Continued.

Species[1]	Method of dispersal	Source
Eleocharis dulcis Trin. ex Hensch.	cultivated for tubers (Chinese water chestnut), rice agriculture	Kern, 1974; Bailey & Bailey, 1976; Everett, 1980–1982; Gordon-Gray, 1995; Brickell & Zuk, 1997; Holm et al., 1997; Huxley, 1992; Turner & Wasson, 1998; Darke, 1999
Eleocharis interstincta (Vahl) Roem. & Schult.	ornamental	Bailey, 1935
Eleocharis lanceolata Fernald	rice agriculture	Smith, 2002c
Eleocharis macrostachya Britton	construction equipment	Bryson, pers. obs.
Eleocharis montevidensis Kunth	ornamental	Brickell & Zuk, 1997
Eleocharis nodulosa (Roth) Schult.	wool casual	Sell & Murrell, 1996
Eleocharis ovata (Roth) Roem. & Schult.	ornamental	Bailey, 1935
Eleocharis pachycarpa E. Desv. in C. Gay	sheep industry	Svenson, 1957
Eleocharis palustris (L.) Roem. & Schult.	ornamental, rice agriculture	Huxley, 1992; Holm et al., 1997
Eleocharis parvula (Roem. & Schult.) Link ex Bluff, Nees & Schauer	ornamental	Everett, 1980–1982
Eleocharis pusilla R. Br.	ornamental	Grounds, 1989
Eleocharis vivipara Link	ornamental	Everett, 1980–1982; Huxley, 1992
Eriophorum angustifolium Honck.	ornamental	Everett, 1980–1982; Grounds, 1989; Huxley, 1992; Turner & Wasson, 1998; Darke, 1999
Eriophorum chamissonis C. A. Mey.	ornamental	Huxley, 1992
Eriophorum gracile W. D. J. Koch ex Roth	ornamental	Darke, 1999
Eriophorum latifolium Hoppe	ornamental	Everett, 1980–1982
Eriophorum vaginatum L.	ornamental	Grounds, 1989; Huxley, 1992; Darke, 1999
Eriophorum virdicarinatum (Engelm.) Fernald	ornamental	Everett, 1980–1982; Grounds, 1989; Huxley, 1992; Darke, 1999
Eriophorum virginicum L.	ornamental	Darke, 1999
Eriophorum scheuchzeri Hoppe	ornamental	Huxley, 1992
Fimbristylis annua (All.) Roem. & Schult.	rice agriculture	Kral, 1971; Holm et al., 1977; Kral, 2002b
Fimbristylis cymosa R. Br.	revegetation	Fosberg, 1988
Fimbristylis decipiens Kral	rice agriculture	Kral, 1971
Fimbristylis dichotoma (L.) Vahl	rice agriculture	Kral, 2002b
Fimbristylis miliacea (L.) Vahl	rice agriculture, soil improvement	Burkill, 1935; Kral, 1971; Holm et al., 1977; Koyama, 1985; Kral, 2002b
Fimbristylis pauciflora R. Br.	soil improvement	Burkill, 1935
Fimbristylis spadicea Vahl	ballast	Smith, 1867
Fimbristylis squarrosa Vahl	ballast	Kral, 2002b

Species[1]	Method of dispersal	Source
Fimbristylis tomentosa Vahl	rice agriculture	Kral, 2002b
Fimbristylis umbellaris (Lam.) Vahl	soil improvement	Burkill, 1935
Fimbristylis vahlii (Lam.) Link	ballast	Smith, 1867
Fuirena squarrosa Michx.	ballast	Smith, 1867
Fuirena umbellata Rottb.	erosion control	Burkill, 1935
Gahnia procera J. R. Forst. & G. Forst.	ornamental	Grounds, 1989
Isolepis cernua (Vahl) Roem. & Schult.	ornamental	Bailey, 1935; Everett, 1980–1982; Grounds, 1989; Greenlee & Fell, 1992; Huxley, 1992; Turner & Wasson, 1998; Darke, 1999
Isolepis nodosa (Rottb.) R. Br.	ornamental	Turner & Wasson, 1998
Isolepis prolifera (Rottb.) R. Br.	ornamental	Huxley, 1992
Isolepis setacea (L.) R. Br.	ornamental	Huxley, 1992
Kobresia pygmaea C. B. Clarke in Hook. f.	erosion control	Dickoré, 1994
Kyllinga brevifolia Rottb.	pine-bark mulch, rice agriculture, turfgrass sod, wool alien	Koyama, 1985; Bryson & Carter, 1992; Sell & Murrell, 1996; Holm et al., 1997; Bryson et al., 1997
Kyllinga erecta Schumach.	wool alien	Sell & Murrell, 1996
Kyllinga gracillima Miq.	turfgrass sod	Bryson et al., 1997
Kyllinga nemoralis (J. R. Forst. & G. Forst.) Dandy ex Hutch. & Dalziel	ornamental	Bailey, 1935
Kyllinga odorata Vahl	wool alien, turfgrass sod	Sell & Murrell, 1996; Bryson et al., 1997
Kyllinga squamulata Thonn. ex Vahl	turfgrass sod	Bryson et al., 1997
Lepironia articulata (Retz.) Domin	fibers in sails and as packing material	Mabberley, 1997
Lipocarpha maculata (Michx.) Torr.	ballast	Smith, 1867
Lipocarpha micrantha (Vahl) G. C. Tucker	ballast	Smith, 1867
Machaerina sinclairii (Hook. f.) Koyama	ornamental	Grounds, 1989
Mapania cuspidata (Miq.) Uittien	ornamental	Bailey, 1935; Simpson, 1992; Simpson & Inglis, 2001
Mapania mannii C. B. Clarke	ornamental	Simpson, 1992; Simpson & Inglis, 2001
Mapania palustris (Hassk. ex Steud.) Fern.-Vill.	ornamental	Simpson, 1992; Simpson & Inglis, 2001
Mapania pandanophylla (F. Muell.) K. Schum.	ornamental	Bailey, 1935
Oreobolus pectinatus Hook. f.	ornamental	Grounds, 1989
Rhynchospora alba (L.) Vahl	ornamental	Bailey, 1935
Rhynchospora colorata (L.) H. Pfeiff.	ornamental	Simpson & Inglis, 2001
Rhynchospora corymbosa (L.) Britton	revegetation, soil improvement	Burkill, 1935

Appendix 1. Continued.

Species[1]	Method of dispersal	Source
Rhynchospora fusca (L.) W. T. Aiton	ornamental	Bailey, 1935
Rhynchospora nervosa (Vahl) Boeckeler	ornamental	Huxley, 1992; Simpson 1993; Simpson & Inglis, 2001
Rhynchospora nervosa subsp. *ciliata* T. Koyama	ornamental	Huxley, 1992
Schoenoplectus acutus (Muhl. ex J. M. Bigelow) Á. Löve & D. Löve	ornamental	Everett, 1980–1982
Schoenoplectus californicus (C. A. Mey.) Soják	erosion control	Smith et al., 1993
Schoenoplectus grossus (L. f.) Palla	rice agriculture	Holm et al., 1997
Schoenoplectus heterochaetus (Chase) Soják	ornamental	Everett, 1980–1982
Schoenoplectus lacustris (L.) Palla	ornamental	Bailey, 1935; Everett, 1980–1982
Schoenoplectus lacustris subsp. *validus* (Vahl) T. Koyama	ornamental	Everett, 1980–1982; Turner & Wasson, 1998
Schoenoplectus mucronatus (L.) Palla	rice agriculture, planted as waterfowl food	Holm et al., 1997; Smith, 2002b
Schoenoplectus tabernaemontani (C. C. Gmel.) Palla	ornamental	Everett, 1980–1982; Grounds, 1989; Greenlee & Fell, 1992; Huxley, 1992; Turner & Wasson, 1998; Darke, 1999
Schoenus pauciflorus (Hook. f.) Hook. f.	ornamental	Grounds, 1989; Huxley, 1992
Scirpus atrovirens Willd.	ornamental	Bailey, 1935; Darke, 1999
Scirpus cyperinus (L.) Kunth	ornamental	Everett, 1980–1982; Huxley, 1992; Darke, 1999
Scirpus divaricatus Elliott	railroad adventive	Mühlenbach, 1979
Scirpus georgianus R. M. Harper	railroad adventive	Mühlenbach, 1983
Scirpus holoschoenus L.	ornamental	Bailey, 1935; Huxley, 1992; Brickell & Zuk, 1997
Scirpus pallidus (Britton) Fernald	accidental transport	Whittemore & Schuyler, 2002
Scirpus pendulus Muhl.	accidental transport	Whittemore & Schuyler, 2002
Scirpus sylvaticus L.	ornamental	Huxley, 1992
Trichophorum alpinum (L.) Pers.	ornamental	Huxley, 1992
Uncinia divaricata W. Boott	ornamental	Grounds, 1989
Uncinia egmontiana Hamlin	ornamental	Grounds, 1989; Greenlee & Fell, 1992; Huxley, 1992
Uncinia rubra Colenso ex Boott	ornamental	Grounds, 1989; Huxley, 1992; Brickell & Zuk, 1997
Uncinia uncinata (L. f.) Kük.	ornamental	Grounds, 1989; Greenlee & Fell, 1992; Brickell & Zuk, 1997; Turner & Wasson, 1998

[1] Plant nomenclature follows *Flora of North America,* volume 23; plant names were also verified through the Missouri Botanical Garden w[3] TROPICOS VAST database (rev. 1.5) (http://mobot.mobot.org/W3T/Search/vast.html) and the International Plant Names Index (http://www.ipni.org/index.html). A more inclusive list of names cited in the references is available from the authors.

APPENDIX 2

Cyperaceous weeds of the world with data on habit, habitat, and distribution.

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Abildgaardia ovata (Burm. f.) Kral	Holm et al., 1979; Soerjani et al., 1987; Moody, 1989; Kukkonen, 2001	P	pastures, rice fields	AFR, ASI, AUS, CAR, EUR, IND, NA, PI, SA
Bolboschoenus affinis (Roth) Drobow	Kukkonen, 2001	P	rice fields	EUR, IND
Bolboschoenus caldwellii (V. J. Cook) Soják	Kern, 1974; Simpson & Inglis, 2001	P	aquatic, irrigation ditches	AUS, PI
Bolboschoenus fluviatilis (Torr.) Soják	Holm et al., 1979; WSSA, 1989	P	aquatic	ASI, AUS, NA
Bolboschoenus maritimus (L.) Palla	Kern, 1974; Reed, 1977; Kühn, 1982; Moody, 1989; Holm et al., 1997; Johnson, 1997; Kissman, 1997	P	aquatic, crops, rice fields	AFR, ASI, CAR, EUR, IND, NA, PI, SA
Bolboschoenus planiculmis (F. Schmidt) T. V. Egorova	Zhirong et al., 1990	P	wetlands, rice fields	ASI
Bulbostylis barbata (Rottb.) C. B. Clarke	Ohwi, 1965; Lin, 1968; Reed, 1977; Godfrey & Wooten, 1979; Holm et al., 1979; Kühn, 1982; Moody, 1989; Le Bourgeois & Merlier, 1995; Simpson & Inglis, 2001	A	crops, cultivated fields, fallow fields, rice fields, waste places	AFR, ASI, AUS, CAR, IND, NA, PI, SA
Bulbostylis capillaris (L.) C. B. Clarke	Godfrey & Wooten, 1979; Lorenzi, 1982; Moody, 1989; Kissman, 1997	A	roadsides, waste places	NA, SA
Bulbostylis ciliatifolia (Elliott) Fernald	Godfrey & Wooten, 1979	A	fallow fields, roadsides, waste places	CAR, NA
Bulbostylis densa (Wall.) Hand.-Mazz.	Ohwi, 1965; Reed, 1977; Kühn, 1982; Moody, 1989; Kukkonen, 2001; Simpson & Inglis, 2001	A	aquatic biotypes, crops, cultivated fields, rice fields, waste places	AFR, ASI, AUS, IND, PI
Bulbostylis filamentosa (Vahl) C. B. Clarke	Healy & Edgar, 1980	P		AFR
Bulbostylis hispidula (Vahl) R. W. Haines	Kühn, 1982; Le Bourgeois & Merlier, 1995; Simpson & Inglis, 2001	A	aquatic biotypes, crops, cultivated fields, grasslands	AFR
Bulbostylis hispidula subsp. *pyriformis* (Lye) R. W. Haines	Gordon-Gray, 1995	A	pioneers or exposed areas, weeds of cultivation	AFR
Bulbostylis humilis (Kunth) C. B. Clarke	Gordon-Gray, 1995	A	gardens, potted plants	AFR
Bulbostylis puberula (Poir.) Kunth	Holm et al., 1979; Soerjani et al., 1987; Moody, 1989		rice fields	IND
Carex acuta L.	Holm et al., 1979	P		EUR
Carex albolutescens Schwein.	WSSA, 1989	P	moist soils	NA
Carex albula Allan	Moore & Edgar, 1970; Simpson & Inglis, 2001	P	crops, grasslands	PI

Appendix 2. Continued.

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Carex aquatilis Wahlenb.	Holm et al., 1979; WSSA, 1989	P	stream margins, wetlands	ASI, NA
Carex atherodes Spreng.	Holm et al., 1979; WSSA, 1989	P	wetlands	NA
Carex aureolensis Steud.	Bryson, pers. obs.	P	crop borders, lawns, pastures, waste places	NA
Carex baccans Nees	Holm et al., 1979	P		PI
Carex biwensis Franch.	Reed, 1977	P	aquatic	ASI
Carex blanda Dewey	Bryson, 1985a; DeFelice & Bryson, 2004	P	lawns, waste places	NA
Carex bonariensis Desf.	Holm et al., 1979; Kissman, 1997	P		SA
Carex breviculmis R. Br.	Moore & Edgar, 1970; Moody, 1989; Simpson & Inglis, 2001	P	rice fields, gardens, grasslands	ASI, AUS, PI
Carex brevicuspis C. B. Clarke	Lin, 1968; Reed, 1977	P		ASI
Carex brizoides L.	Reed, 1977; Kühn, 1982	P	crops, grasslands	ASI, EUR
Carex brongniartii Kunth	Holm et al., 1979	P		SA
Carex buchananii Berggr.	Moore & Edgar, 1970; Simpson & Inglis, 2001	P	grasslands	PI
Carex canescens L.	Holm et al., 1979	P	wetlands	EUR
Carex cherokeensis Schwein.	WSSA, 1989; DeFelice & Bryson, 2004	P	lawns, pastures	NA
Carex comans Berggr.	Moore & Edgar, 1970; Simpson & Inglis, 2001	P	gardens, pastures	PI
Carex comosa Boott	Bryson, pers. obs.	P	wetlands	NA
Carex coriacca Hamlin	Moore & Edgar, 1970; Simpson & Inglis, 2001	P	grasslands	PI
Carex dietrichiae Boeckeler	Holm et al., 1979	P		SA
Carex dimorpholepis Steud.	Ohwi, 1965	P	wet fields	ASI
Carex dispalata Boott ex A. Gray	Reed, 1977	P	aquatic, wet/low places	ASI
Carex disticha Huds.	Holm et al., 1979	P		EUR
Carex divisa Huds.	Holm et al., 1979; Kukkonen, 2001	P	gardens, rice fields	AFR, ASI, AUS (New Zealand), EUR, IND, NA
Carex divulsa Stokes	Holm et al., 1979	P	grasslands	EUR, PI, SA
Carex eurycarpa T. Holm	Holm et al., 1979; WSSA, 1989	P		NA
Carex fedia Nees	Moody, 1989	P	rice fields	ASI
Carex flagellifera Colenso	Healy & Edgar, 1980; Parsons & Cuthbertson, 1992; Simpson & Inglis, 2001	P	pastures	PI

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Carex foliosa D. Don	Moody, 1989; Kukkonen, 2001	P	rice fields	ASI, IND
Carex frankii Kunth	WSSA, 1989	P	crop borders, lawns, pastures, waste places	NA
Carex gayana E. Desv.	Kissman, 1997	P		SA
Carex glauca Scop.	Holm et al., 1979	P		ASI
Carex glaucescens Elliott	WSSA, 1989	P	pastures, roadsides, waste places	NA
Carex graeffeana Boeckeler	Holm et al., 1979	P		PI
Carex heterostachya Bunge	Zhirong et al., 1990	P	field borders, wetlands	ASI
Carex hirta L.	Kühn, 1982	P	crops, grasslands, waste places	AFR, ASI, EUR, NA
Carex hudsonii A. Benn.	Holm et al., 1979	P		EUR
Carex inversa R. Br.	Healey & Edgar, 1980; Simpson & Inglis, 2001	P	gardens	PI
Carex iynx Nelmes	Healy & Edgar, 1980; Simpson & Inglis, 2001	P	grasslands	PI
Carex kobomugi Ohwi	Small, 1954; Svenson, 1979; Stalter, 1980; Standley, 1983	P	sandy beaches	ASI, NA
Carex lacustris Willd.	Holm et al., 1979; WSSA, 1989	P	ditches, roadsides, wetlands	NA
Carex lasiocarpa Ehrh.	Holm et al., 1979; Kühn, 1982; WSSA, 1989; Simpson & Inglis, 2001	P	aquatic biotypes	ASI, EUR, NA
Carex leavenworthii Dewey	Bryson, 1985a	P	lawns, waste places	NA
Carex leporina L.	Holm et al., 1979; Kühn, 1982	P	grasslands, waste places	AFR, ASI, EUR
Carex longebrachiata Boeckeler	Reed, 1977; Simpson & Inglis, 2001	P	grasslands, wet places	AUS, PI
Carex longii Mack.	Bryson, 1985a	P	lawns, pastures, waste places	NA
Carex louisianica L. H. Bailey	WSSA, 1989	P	ditches, right-of-ways, roadsides, wetlands	NA
Carex lucida Boott	Reed, 1977	P	low places/ elevations	PI
Carex lupulina Muhl. ex Willd.	Holm et al., 1979; WSSA, 1989	P	ditches, roadsides, wetlands	NA
Carex macrorrhiza Boeckeler	Kissman, 1997	P		SA
Carex maorica Hamlin	Moore & Edgar, 1970; Simpson & Inglis, 2001	P	aquatic, irrigation ditches	PI
Carex maximowiczii Miq.	Reed, 1977	P	wet places	ASI
Carex myosurus Nees	Holm et al., 1979	P		AUS, PI

Appendix 2. Continued.

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Carex nebrascensis Dewey	USDA, 1970; Holm et al., 1979; WSSA, 1989	P	pastures, roadsides	NA
Carex nigra (L.) Reichard	Holm et al., 1979	P	stream and lake margins, wetlands	EUR, NA
Carex notha Kunth	Moody, 1989	P	rice fields	ASI
Carex nubigena D. Don ex Tilloch & Taylor	Holm et al., 1979; Moody, 1989	P	rice fields	ASI
Carex oklahomensis Mack.	Bryson et al., 1992, 1994b, 1996; Standley, 2002	P	pastures, roadsides, waste places	NA
Carex ovalis Gooden.	Kühn, 1982; Simpson & Inglis, 2001	P	forests, grasslands, waste places	EUR, NA
Carex pallescens L.	WSSA, 1989	P	lawns, waste places	ASI, EUR, NA, PI
Carex panicea L.	Kühn, 1982	P	aquatic biotypes, crops, grasslands	AFR, ASI, EUR, NA, PI
Carex paniculata L.	Reed, 1977; Holm et al., 1979; Kühn, 1982; Simpson & Inglis, 2001	P	aquatic biotypes, waste places	AFR, ASI, AUS, EUR
Carex philocrena V. I. Krecz	Moody, 1989	P	rice fields	ASI
Carex praegracilis W. Boott	Reznicek et al., 1976; Swink & Wilhelm, 1979; Bruton & Catling, 1982; Reznicek & Catling, 1987	P	waste places, roadsides	NA
Carex pruinosa Boott	Moody, 1989	P	rice fields	ASI
Carex pumila Thunb.	Lin, 1968; Holm et al., 1979	P		ASI, PI
Carex pycnostachya Kar. & Kir.	Kukkonen, 2001	P	rice fields	ASI, IND
Carex remota L.	Holm et al., 1979	P		ASI
Carex rigescens (Franch.) V. I. Krecz.	Zhirong et al., 1990	P	lawns, orchards, waste places	ASI
Carex riparia Curtis	Holm et al., 1979	P		EUR
Carex rostrata Stokes ex With.	WSSA, 1989	P	wetlands	
Carex sahnii Ghildyal & U. C. Bhattach.	Moody, 1989	P	rice fields	ASI
Carex senta Boott	Holm et al., 1979; WSSA, 1989	P	stream and river margins, wetlands	NA
Carex sororia Kunth	Kissman, 1997	P		SA
Carex spicata Huds.	Bryson, pers. obs.	P		ASI, EUR, NA
Carex testacea Sol. ex Boott	Parsons & Cuthbertson, 1992; Simpson & Inglis, 2001	P	pastures	PI
Carex thunbergii Steud.	Ohwi, 1965; Reed, 1977	P	aquatic, rice fields	ASI
Carex uruguensis Boeckeler	Kissman, 1997	P	pastures, roadsides	SA
Carex verrucosa Muhl.	WSSA, 1989	P	roadsides, wet areas	NA
Carex vulpina L.	Holm et al., 1979	P		EUR
Carex vulpinoidea Michx.	Moore & Edgar, 1970; Godfrey & Wooten, 1979; Simpson & Inglis, 2001	P	pastures, old fields, waste places	EUR, NA, PI, SA

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Cladium jamaicense Crantz	Holm et al., 1979	P	aquatic	NA
Cladium mariscus (L.) Pohl	Holm et al., 1979; Kühn, 1982; Moody, 1989; Simpson & Inglis, 2001	P	aquatic biotypes, rice fields	AFR, ASI, EUR, IND, NA, PI, SA
Courtoisina cyperoides (Roxb.) Soják	Simpson & Koyama, 1998; Simpson & Inglis, 2001	A	rice fields	AFR, ASI, IND
Cyperus acuminatus Torr. & Hook.	DeFelice & Bryson, 2004	A	field borders, pastures, roadsides, wet clay soils	NA
Cyperus aggregatus (Willd.) Endl.	Holm et al., 1979; Kühn, 1982; Lorenzi, 1982; WSSA, 1989; Wilson, 1993; Kissman, 1997; Simpson & Inglis, 2001	P	crops, sandy soil, waste places	AUS, CAR, NA, SA
Cyperus albostriatus Schrad.	Healy & Edgar, 1980; Simpson & Inglis, 2001	P	gardens, waste places	AUS, PI
Cyperus alopecuroides Rottb.	Holm et al., 1979; Kühn, 1982; Moody, 1989; Carter et al., 1996; Bryson et al., 1998; Simpson & Inglis, 2001	P	aquatic biotypes, rice fields	AFR, ASI, AUS, IND, NA, PI, SA
Cyperus alternifolius L. subsp. *flabelliformis* Kük.	Kern, 1974; Holm et al., 1979; Kühn, 1982; Moody, 1989; Kissman, 1997; Simpson & Inglis, 2001	P	aquatic biotypes, rice fields, waste places	AFR, ASI, EUR, IND, NA, PI, SA
Cyperus alulatus J. Kern	Moody, 1989; Kukkonen, 2001	A	rice fields	ASI, IND
Cyperus amabilis Vahl	Holm et al., 1979; Kühn, 1982; Le Bourgeois & Merlier, 1995; Simpson & Inglis, 2001	A	grasslands, waste places	AFR, ASI, IND, SA
Cyperus amuricus Maxim.	Ohwi, 1965; Reed, 1977; Holm et al., 1979	A/P	cultivated fields, waste places, wet places	ASI
Cyperus arenarius Retz.	Simpson & Inglis, 2001	P	unspecified	ASI, IND
Cyperus articulatus L.	Holm et al., 1979; Kühn, 1982; Moody, 1989; WSSA, 1989; Kissman, 1997; Bryson et al., 1998; Simpson & Inglis, 2001	P	aquatic biotypes, crops, rice fields	AFR, ASI, AUS, IND, NA, SA
Cyperus babakan Steud.	Kern, 1974; Holm et al., 1979; Soerjani et al., 1987; Moody, 1989	P	rice fields	ASI, IND, PI
Cyperus bifax C. B. Clarke	Koyama, 1985; Moody, 1989; Wilson, 1993	P	ditches, irrigated cultivation, open wet ground, rice fields	ASI, AUS, IND
Cyperus boreohemisphaericus Lye	Simpson & Inglis, 2001		crops	AFR
Cyperus bulbosus Vahl	Terry, 1976; Reed, 1977; Holm et al., 1979; Moody, 1989; Kukkonen, 2001; Simpson & Inglis, 2001	P	grasslands, rice fields	AFR, ASI, AUS, IND
Cyperus castaneus Willd.	Holm et al., 1979; Moody, 1989	A	rice fields	ASI

Appendix 2. Continued.

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Cyperus cephalotes Vahl	Soerjani et al., 1987; Moody, 1989	P	rice fields	ASI, IND
Cyperus compactus Retz.	Kern, 1974; Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Kukkonen, 2001; Simpson & Inglis, 2001	P	aquatic biotypes, crops, ditches, rice fields, waste places, wet places	ASI, AUS, IND, PI
Cyperus compressus L.	Ohwi, 1965; Lin, 1968; Kern, 1974; Godfrey & Wooten, 1979; Kühn, 1982; Koyama, 1985; Soerjani et al., 1987; Moody, 1989; WSSA, 1989; Wagner & Herbst, 1995; Bryson et al., 1998; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002; DeFelice & Bryson, 2004	A	crops, fallow rice fields, gardens, grasslands, lawns, roadsides, waste places	AFR, ASI, AUS, IND, NA, PI, SA
Cyperus congestus Vahl	Healey & Edgar, 1980; Wilson, 1993; Gordon-Gray, 1995; Simpson & Inglis, 2001	P	cultivation, damp ground, disturbed areas, ditches, gardens, roadsides	AFR, AUS
Cyperus conglomeratus Rottb.	Moody, 1989; Simpson & Inglis, 2001	P	crops, rice fields	AFR, IND
Cyperus corymbosus Rottb.	Holm et al., 1979; Moody, 1989; Simpson & Inglis, 2001	P	rice fields	ASI, IND, SA
Cyperus crassipes Vahl	Reed, 1977; Holm et al., 1979	P		AFR
Cyperus croceus Vahl	Godfrey & Wooten, 1979; WSSA, 1989; Bryson et al., 1998	P	pastures, turf, waste places	CAR, NA, SA
Cyperus cuspidatus Kunth	Kern, 1974; Godfrey & Wooten, 1979; Kühn, 1982; Moody, 1989; WSSA, 1989; Kukkonen, 2001; Simpson & Inglis, 2001	A	aquatic biotypes, crops, fallow fields, rice fields, sandy fields, waste places, wet places	AFR, ASI, AUS, IND, NA, PI, SA
Cyperus cyperinus (Retz.) Suringar	Lin, 1968; Reed, 1977; Simpson & Koyama, 1998; Simpson & Inglis, 2001	P	cultivated lands, gardens, rice fields, waste places	ASI, IND, PI
Cyperus cyperoides (L.) Kuntze	Kern, 1974; Terry, 1976; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Zhirong et al., 1990; Gordon-Gray, 1995; Le Bourgeois & Merlier, 1995; Johnson, 1997; Simpson & Koyama, 1998; Kukkonen, 2001; Simpson & Inglis, 2001	P	crops, disturbed sites, fallow fields, fields, gardens, grasslands, rice fields, roadsides, waste places	AFR, ASI, AUS, CAR, IND, PI
Cyperus cyperoides subsp. *macrocarpus* (Kunth) Lye	Terry, 1976	P	crops	AFR
Cyperus denudatus L. f.	Simpson & Inglis, 2001	P	rice fields	AFR
Cyperus diandrus Torr.	Holm et al., 1979	A	wet areas	NA
Cyperus diaphanus Schrad. ex Roem. & Schult.	Kern, 1974; Moody, 1989	A	rice fields	ASI, IND, PI

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Cyperus difformis L.	Ohwi, 1965; Lin, 1968; Kern, 1974; Terry, 1976; Reed, 1977; Holm et al., 1977, 1979; DeFilipps, 1980c; Moody, 1981; Kühn, 1982; Koyama, 1985; Akobundu & Agyakwa, 1987; Soerjani et al., 1987; Moody, 1989; WSSA, 1989; Zhirong et al., 1990; Gordon-Gray, 1995; Johnson, 1997; Kissman, 1997; Bryson et al., 1998; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002; Carter, 2005	A	aquatic biotypes, crops, grasslands, rice fields	AFR, ASI, AUS, EUR, IND, NA, PI, SA
Cyperus diffusus Vahl	Cardenas et al., 1972; Reed, 1977; Holm et al., 1979; Moody, 1989; Kissman, 1997; Simpson & Koyama, 1998; Simpson & Inglis, 2001; DeFelice & Bryson, 2004	P	gardens, low elevations, rice fields, warm regions	ASI, CAR, IND, PI, SA
Cyperus digitatus Roxb.	Kern, 1974; Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Simpson & Koyama, 1998; Kukkonen, 2001; Simpson & Inglis, 2001	P	aquatic biotypes, crops, rice fields, waste places	AFR, ASI, AUS, IND, NA, PI, SA
Cyperus dilatatus Schumach.	Simpson & Inglis, 2001	P	cultivated fields, gardens	AFR
Cyperus distans L. f.	Kern, 1974; Terry, 1976; Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Gordon-Gray, 1995; Johnson, 1997; Kissman, 1997; Simpson & Koyama, 1998; Simpson & Inglis, 2001	P	aquatic biotypes, crops, grasslands, rice fields, waste places	AFR, ASI, AUS, CAR, EUR, IND, NA, PI, SA
Cyperus distinctus Steud.	Carter, pers. obs.	P	ditches, roadsides, waste places	CAR, NA
Cyperus dives Delile	Gordon-Gray, 1995	P	sugarcane fields	AFR
Cyperus dubius Rottb.	Moody, 1989; Gordon-Gray, 1995; Simpson & Inglis, 2001	P	open rice fields, sandy sites	AFR, IND
Cyperus duclouxii E. G. Camus	Zhirong et al., 1990	P		ASI
Cyperus echinatus (L.) A. W. Wood	WSSA, 1989; Bryson et al., 1998	P	ditches, pastures, roadsides, waste places	NA
Cyperus elatus L.	Kern, 1974; Soerjani et al., 1987; Moody, 1989; Simpson & Inglis, 2001	P	rice fields	ASI, IND, PI
Cyperus elegans L.	Bryson et al., 1998	P	waste places	CAR, NA
Cyperus entrerianus Boeckeler	Kissman, 1997; Carter, 1990; Carter & Jones, 1991; Bryson & Carter, 1994, 1996; Bryson et al., 1998; Simpson & Inglis, 2001; DeFelice & Bryson, 2004	P	crops, pastures, roadsides	NA, SA

Appendix 2. Continued.

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Cyperus eragrostis Lam.	Holm et al., 1979; Parsons & Cuthbertson, 1992; Wilson, 1993; Gordon-Gray, 1995; Kissman, 1997; Bryson et al., 1998; Simpson & Koyama, 1998; Simpson & Inglis, 2001	P/A?	disturbed or fallow areas, pastures, rice fields, roadsides	AFR, AUS, EUR, NA, PI, SA
Cyperus erythrorhizos Muhl.	Holm et al., 1979; Moody, 1989; WSSA, 1989; Bryson et al., 1998; DeFelice & Bryson, 2004	A	rice fields, wet areas	ASI, NA
Cyperus esculentus L.	USDA, 1970; Kern, 1974; Terry, 1976; Holm et al., 1977; Godfrey & Wooten, 1979; Holm et al., 1979; Kühn, 1982; Lorenzi, 1982; Moody, 1989; WSSA, 1989; Gordon-Gray, 1995; Le Bourgeois & Merlier, 1995; Johnson, 1997; Kissman, 1997; Bryson et al., 1998; Simpson & Koyama, 1998; Kukkonen, 2001; Simpson & Inglis, 2001; DeFelice & Bryson, 2004; Rzedowski & Rzedowski, 2004; Carter, 2005	P	crops, fields, irrigated fields, pastures, rice fields, turf, waste places	AFR, ASI, AUS, CAR, EUR, IND, NA, PI, SA
Cyperus exaltatus Retz.	Holm et al., 1979; Koyama, 1985; Moody, 1989; Johnson, 1997; Kukkonen, 2001; Simpson & Inglis, 2001	P	low wet sites, rice fields	AFR, AUS, IND
Cyperus fasciculatus Elliott	Holm et al., 1979			ASI
Cyperus flavescens L.	Holm et al., 1979; Soerjani et al., 1987; Gordon-Gray, 1995; Johnson, 1997; Kukkonen, 2001	A	crops, pastures, rice fields, roadside ditches, seeps, turf, waste places	AFR, ASI, CAR, EUR, IND, NA, SA
Cyperus flavicomus Michx.	Godfrey & Wooten, 1979; Holm et al., 1979; Johnson, 1997; Bryson et al., 1998	A	crops, pastures, rice fields, turf, waste places	AFR, ASI, NA, SA
Cyperus flavidus Retz.	Lin, 1968; Kern, 1974; Reed, 1977; Holm et al., 1979; Moody, 1989; Zhirong et al., 1990; Simpson & Koyama, 1998; Simpson & Inglis, 2001	A/P	crops, fallow fields, rice fields, wet places	AFR, ASI, AUS, IND, PI
Cyperus floribundus (Kük.) R. Carter & S. D. Jones	Carter & Jones, 1997; Carter, pers. obs.	A/P	agricultural fields, disturbed sites, roadsides	NA
Cyperus foliaceus C. B. Clarke	Simpson & Inglis, 2001	A	rice fields	AFR
Cyperus friburgensis Boeckeler	Kissman, 1997	P		SA
Cyperus fulvus R. Br.	Holm et al., 1979	P		SA
Cyperus fuscus L.	Holm et al., 1979; WSSA, 1989; Zhirong et al., 1990; Kukkonen, 2001; Simpson & Inglis, 2001	A	crops, moist fields, rice fields, wet areas	AFR, ASI, EUR, NA

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Cyperus giganteus Vahl	Kissman, 1997	P		SA
Cyperus glaber L.	Kukkonen, 2001	A	moist fields	ASI, EUR, IND
Cyperus glomeratus L.	Zhirong et al., 1990; Kukkonen, 2001	A/P	rice fields, wetlands	ASI, EUR, IND
Cyperus gracilis R. Br.	Holm et al., 1979	P		AUS, PI
Cyperus gracilinux C. B. Clarke	Holm et al., 1979	P		AFR
Cyperus grandibulbosus C. B. Clarke	Terry, 1976; Simpson & Inglis, 2001	P	unspecified	AFR
Cyperus hakonensis Franch. & Sav.	Holm et al., 1979			ASI
Cyperus haspan L.	Ohwi, 1965; Lin, 1968; Kern, 1974; Holm et al., 1979; Kühn, 1982; Koyama, 1985; Akobundu & Agyakwa, 1987; Soerjani et al., 1987; Moody, 1989; Zhirong et al., 1990; Johnson, 1997; Kissman, 1997; Simpson & Koyama, 1998; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	A/P	grasslands, crops, aquatic biotypes, rice fields	AFR, ASI, AUS, IND, NA, PI, SA
Cyperus hermaphroditus (Jacq.) Standl.	Holm et al., 1979; Kissman, 1997	P		NA, SA
Cyperus hyalinus Vahl	WSSA, 1989; Simpson & Inglis, 2001	A	gardens, turf	AFR, ASI, AUS, IND, NA
Cyperus imbricatus Retz.	Kern, 1974; Reed, 1977; Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Zhirong et al., 1990; Kissman, 1997; Simpson & Inglis, 2001	P	aquatic biotypes, crops, rice fields	AFR, ASI, CAR, IND, NA, PI, SA
Cyperus intactus Vahl	Gordon-Gray, 1995	A/P	disturbed grasslands	AFR
Cyperus iria L.	Ohwi, 1965; Lin, 1968; Kern, 1974; Holm et al., 1977, 1979; Moody, 1981; Kühn, 1982; Lorenzi, 1982; Koyama, 1985; Akobundu & Agyakwa, 1987; Soerjani et al., 1987; Moody, 1989; WSSA, 1989; Zhirong et al., 1990; Gordon-Gray, 1995; Johnson, 1997; Kissman, 1997; Bryson et al., 1998; Simpson & Koyama, 1998; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002; DeFelice & Bryson, 2004; Carter, 2005	A/P	aquatic biotypes, crops, rice fields, waste places	AFR, ASI, AUS, CAR, EUR, IND, NA, PI, SA
Cyperus javanicus Houtt.	Holm et al., 1979; Moody, 1989	P	rice fields	ASI, IND, PI
Cyperus laetus J. Presl & C. Presl	Holm et al., 1979; Kissman, 1997	P		SA
Cyperus laevigatus L.	Holm et al., 1979; Kühn, 1982; Moody, 1989; Simpson & Inglis, 2001	P	aquatic biotypes, rice fields	AFR, ASI, AUS, CAR, EUR, IND, NA, PI, SA

Appendix 2. Continued.

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Cyperus lanceolatus Poir.	Holm et al., 1979; Lorenzi, 1982; Akobundu & Agyakwa, 1987; Johnson, 1997; Kissman, 1997	P	ditches, rice fields, roadsides	AFR, NA, SA
Cyperus latifolius Poir.	Simpson & Inglis, 2001	P	pastures	AFR
Cyperus lecontei Torr. ex Steud.	WSSA, 1989; Bryson et al., 1998	P	shorelines, waste places	NA
Cyperus ligularis L.	Holm et al., 1979; Kissman, 1997	P		AFR, ASI, NA, SA
Cyperus longibracteatus (Cherm.) Kük.	Akobundu & Agyakwa, 1987	P	forests, rice fields	AFR
Cyperus longus L.	Terry, 1976; Holm et al., 1979; Moody, 1989; Kukkonen, 2001; Simpson & Inglis, 2001	P	aquatic biotypes, crops, rice fields	AFR, ASI, EUR, IND
Cyperus luzulae (L.) Rottb. ex Retz.	Cardenas et al., 1972; Holm et al., 1979; Lorenzi, 1982; Moody, 1989; Kissman, 1997; Simpson & Inglis, 2001	P	cultivated fields, rice fields	SA
Cyperus macrostachyos Lam.	Moody, 1989		rice fields	IND
Cyperus malaccensis Lam.	Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Simpson & Inglis, 2001	P	aquatic biotypes, cultivated fields, rice fields	ASI, AUS, IND, PI
Cyperus mapanioides C. B. Clarke	Simpson & Koyama, 1998; Simpson & Inglis, 2001	P	crops, cultivated fields	AFR
Cyperus maranguensis K. Schum.	Terry, 1976; Holm et al., 1979; Simpson & Inglis, 2001	P	cultivated fields	AFR
Cyperus meyenianus Kunth	Kissman, 1997	P		SA
Cyperus michelianus (L.) Link. subsp. *pygmaeus* (Rottb.) Asch. & Graebn.	Kern, 1974; Holm et al., 1979; Soerjani et al., 1987; Moody, 1989; Zhirong et al., 1990; Kukkonen, 2001; Simpson & Inglis, 2001	A	ditches, cultivated fields, fallow rice fields, gardens, rice fields	AFR, ASI, AUS, EUR, IND, PI
Cyperus microiria Steud.	Ohwi, 1965; Holm et al., 1979; Moody, 1989	A	crops, cultivated fields, rice fields, wetlands	ASI, IND, NA
Cyperus mirus C. B. Clarke	Wilson, 1993	P	gardens	AUS
Cyperus mitis Steud.	Moody, 1989		rice fields	ASI
Cyperus mutisii (Kunth) Andersson	Holm et al., 1979	P		NA, SA
Cyperus nipponicus Franch. & Sav.	Reed, 1977; Holm et al., 1979	A	crops, waste places	ASI
Cyperus niveus Retz.	Reed, 1977; Moody, 1989	P	open forests, rice fields, wet places	ASI, IND
Cyperus novae-hollandiae Boeckeler	Holm et al., 1979			AUS
Cyperus nutans Vahl	Kern, 1974; Moody, 1989; Simpson & Inglis, 2001	P	crops, rice fields	AFR, ASI, IND, PI
Cyperus obtusiflorus Vahl	Simpson & Inglis, 2001	P	gardens	AFR

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Cyperus ochraceus Vahl	Bryson et al., 1996, 1998	P	ditches, roadsides, waste places	CAR, NA, SA
Cyperus odoratus L.	Lin, 1968; Cardenas et al., 1972; Kern, 1974; Holm et al., 1979; Kühn, 1982; Lorenzi, 1982; Soerjani et al., 1987; Moody, 1989; WSSA, 1989; Wagner et al., 1990; Kissman, 1997; Bryson et al., 1998; Simpson & Koyama, 1998; Simpson & Inglis, 2001; DeFelice & Bryson, 2004	A/P	aquatic biotypes, crops, rice fields, taro paddies, waste places	AFR, ASI, AUS, CAR, EUR, IND, NA, PI, SA
Cyperus oxylepis Nees ex Steud.	Godfrey & Wooten, 1979; WSSA, 1989; Bryson et al., 1996, 1998	P	mechanically disturbed sites, waste places, roadsides	NA
Cyperus pangorei Rottb.	Holm et al., 1979; Moody, 1989	P	rice fields	AFR, IND
Cyperus papyrus L.	Holm et al., 1979; Simpson & Inglis, 2001	P	aquatic	AFR, NA
Cyperus pilosus Vahl	Lin, 1968; Kern, 1974; Reed, 1977; Soerjani et al., 1987; Moody, 1989; Zhirong et al., 1990	P	crops, rice fields, waste places	ASI, IND, NA, PI
Cyperus platystylis R. Br.	Kern, 1974; Soerjani et al., 1987; Moody, 1989	P	rice fields	ASI, AUS, IND, PI
Cyperus pohlii (Nees) Steud.	Kissman, 1997	P		SA
Cyperus polystachyos Rottb.	Lin, 1968; Kern, 1974; Reed, 1977; Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Kissman, 1997; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	A/P	aquatic biotypes, crops, fallow rice fields, grasslands, waste places, wet places	AFR, ASI, AUS, EUR, IND, NA, PI, SA
Cyperus polystachyos var. *texensis* (Torr.) Fernald	WSSA, 1989; Bryson et al., 1998	A/P	crops, grasslands, lawns, rice fields, roadsides, waste places, wet places	NA
Cyperus procerus Rottb.	Kern, 1974; Holm et al., 1979; Soerjani et al., 1987; Moody, 1989	P	rice fields	ASI, AUS, IND, PI
Cyperus prolifer Lam.	WSSA, 1989; Carter et al., 1996; Bryson et al., 1998	P	aquatic	AFR, NA
Cyperus prolixus Kunth	Kissman, 1997	P	aquatic	NA, SA
Cyperus pseudosomaliensis Kük.	Simpson & Inglis, 2001	P	gardens	AFR
Cyperus pseudovegetus Steud.	WSSA, 1989; Bryson et al., 1998; Ramos et al., 2004	P	field borders, pastures, wet soil	NA, SA
Cyperus pulcherrimus Willd. ex Kunth	Kern, 1974; Holm et al., 1979; Soerjani et al., 1987; Moody, 1989	P	rice fields	ASI, IND, PI

Appendix 2. Continued.

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Cyperus pumilus L.	Kern, 1974; Holm et al.,1979; Soerjani et al., 1987; Moody, 1989; Kukkonen, 2001; Ravi & Mohanan, 2002	A	disturbed sandy soils, fallow fields, rice fields, waste lands	AFR, ASI, AUS, CAR, IND, NA, PI
Cyperus puncticulatus Vahl	Ravi & Mohanan, 2002	A	rice fields	ASI, IND
Cyperus pustulatus Vahl	Johnson, 1997; Simpson & Inglis, 2001	A	aquatic, rice fields	AFR
Cyperus radians Nees & Meyen	Holm et al., 1979; Kühn, 1982; Moody, 1989; Simpson & Inglis, 2001	P	aquatic biotypes, rice fields, waste places	ASI, PI
Cyperus reduncus Hochst. ex Boeckeler	Holm et al., 1979; Simpson & Inglis, 2001	A		AFR
Cyperus reflexus Vahl	Kissman, 1997	P	pastures, waste places	NA, SA
Cyperus remotispicatus S. S. Hooper	Simpson & Inglis, 2001		rice fields	AFR
Cyperus retroflexus Buckley	Carter et al., 1987; Carter & Bryson, 1991a, b; Carter & Jones, 1997	P	sandy waste places	NA
Cyperus retrorsus Chapm.	WSSA, 1989; Bryson et al., 1998	P	grasslands, turf, waste places	NA
Cyperus rigidifolius Steud.	Terry, 1976; Holm et al., 1979; Gordon-Gray, 1995; Simpson & Inglis, 2001	P	crops, disturbed grassland, gardens, lawns	AFR
Cyperus rotundus L.	Elliott, 1821; Lin, 1968; USDA, 1970; Cardenas et al., 1972; Kern, 1974; Terry, 1976; Holm et al., 1977; Godfrey & Wooten, 1979; Holm et al., 1979; Moody, 1981, 1989; Kühn, 1982; Lorenzi, 1982; Koyama, 1985; Soerjani et al., 1987; WSSA, 1989; Zhirong et al., 1990; Wilson, 1993; Hughes, 1995; Le Bourgeois & Merlier, 1995; Johnson, 1997; Kissman, 1997; Waterhouse, 1997; Bryson et al., 1998; Simpson & Koyama, 1998; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002; DeFelice & Bryson, 2004; Ramos et al., 2004; Rzedowski & Rzedowski, 2004; Carter, 2005	P	crops, gardens, field crops, grasslands, lawns, pastures, rice fields, roadsides, taro, turf, waste places	AFR, ASI, AUS, CAR, EUR, IND, NA, PI, SA
Cyperus rubicundus Vahl	Moody, 1989		rice fields	IND
Cyperus sanguinolentus Vahl	Lin, 1968; Kern, 1974; Reed, 1977; Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Zhirong et al., 1990; Carter & Bryson, 2000b; Kukkonen, 2001; Simpson & Inglis, 2001	A/P	aquatic biotypes, crops, grasslands, rice fields, wet places	AFR, ASI, AUS, IND, NA, PI
Cyperus schweinfurthianus Boeckeler	Holm et al., 1979	P		AFR

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Cyperus seemannianus Boeckeler	Holm et al., 1979			PI
Cyperus serotinus Rottb.	Reed, 1977; Holm et al., 1979; Kühn, 1982; Moody, 1989; Zhirong et al., 1990; Kukkonen, 2001; Simpson & Inglis, 2001	P	aquatic biotypes, crops, rice fields, wet places	AFR, ASI, EUR, IND, NA
Cyperus seslerioides Kunth	Holm et al., 1979	P		NA
Cyperus soyauxii Boeckeler	Simpson & Inglis, 2001	P	cultivated fields	AFR
Cyperus sphacelatus Rottb.	Kern, 1974; Reed, 1977; Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Carter et al., 1996; Johnson, 1997; Kissman, 1997; Bryson et al., 1998; Simpson & Koyama, 1998; Simpson & Inglis, 2001	A/P	aquatic biotypes, crops, grasslands, rice fields, waste places	AFR, ASI, AUS, IND, NA, PI, SA
Cyperus squarrosus L.	Holm et al., 1979; Kühn, 1982; Moody, 1989; Le Bourgeois & Merlier, 1995; Kukkonen, 2001; Simpson & Inglis, 2001	A	aquatic biotypes, crops, forests, gardens, grass-lands, rice fields, waste places	AFR, ASI, AUS, EUR, IND, NA, SA
Cyperus stenophyllus J. V. Suringar	Moody, 1989		rice fields	PI
Cyperus stoloniferus Retz.	Moody, 1989	P	rice fields	ASI
Cyperus strigosus L.	Holm et al., 1979; Moody, 1989; WSSA, 1989; Bryson et al., 1998; Simpson & Inglis, 2001; DeFelice & Bryson, 2004	P	crops, pastures, roadsides, wet areas	ASI, EUR, NA, PI
Cyperus substramineus Kük.	Kern, 1974; Moody, 1989; Ravi & Mohanan, 2002	A/P	rice fields	ASI, IND
Cyperus sulcinux C. B. Clarke	Kern, 1974; Moody, 1989	A	fields, rice fields, roadsides	ASI, AUS, IND, PI
Cyperus surinamensis Rottb.	WSSA, 1989; Kissman, 1997; Bryson et al., 1998	A/P		SA
Cyperus tegetiformis Roxb.	Holm et al., 1979; Moody, 1989		rice fields	AFR, ASI, IND
Cyperus tegetum Roxb.	Holm et al., 1979; Moody, 1989		rice fields	ASI, IND
Cyperus tenellus L. f.	Moore & Edgar, 1970; Simpson & Inglis, 2001		gardens, irrigation ditches	AFR, AUS, PI
Cyperus tenuiculmis Boeckeler	Kern, 1974; Holm et al., 1979; Soerjani et al., 1987; Moody, 1989; Simpson & Inglis, 2001	P	fallow fields, gardens, grass-lands, rice fields	AFR, ASI, AUS, PI
Cyperus tenuis Sw.	Holm et al., 1979; Johnson, 1997; Simpson & Inglis, 2001	P	rice fields	SA
Cyperus tenuispica Steud.	Kern, 1974; Holm et al., 1979; Koyama, 1985; Soerjani et al., 1987; Moody, 1989; Simpson & Koyama, 1998; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	A/P	cultivated fields, rice fields, wet places	AFR, ASI, IND, PI
Cyperus trialatus (Boeckeler) J. Kern	Kern, 1974; Holm et al., 1979; Moody, 1989	P	rice fields, roadsides	ASI, IND, PI

Appendix 2. Continued.

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Cyperus truncatus C. A. Mey. ex Turcz.	Holm et al., 1979			ASI
Cyperus uncinatus Poir.	Holm et al., 1979; Moody, 1989; Simpson & Inglis, 2001		rice fields	PI
Cyperus ustulatus A. Rich.	Moore & Edgar, 1970; Terry, 1976; Simpson & Inglis, 2001		pastures	PI
Cyperus virens Michx.	WSSA, 1989; Kissman, 1997; Bryson et al., 1998	P		NA, SA
Cyperus vorsteri K. L. Wilson	Gordon-Gray, 1995	P	aggressive weed in parks and gardens	AFR
Cyperus zollingeri Steud.	Kern, 1974; Holm et al.,1979; Moody, 1989; Simpson & Inglis, 2001	A	crops, rice fields, roadsides	AFR, ASI, AUS, PI
Eleocharis acicularis (L.) Roem. & Schult.	Ohwi, 1965; Lin, 1968; Kern, 1974; Holm et al., 1979, 1997; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; WSSA, 1989; Simpson & Inglis, 2001	P	aquatic biotypes, crops, grasslands, rice fields	AFR, ASI, AUS, EUR, IND, NA, PI, SA
Eleocharis acuta R. Br.	Holm et al., 1979	P		AUS
Eleocharis acutangula (Roxb.) Schult.	Lin, 1968; Kern, 1974; Reed, 1977; Holm et al., 1979; Kühn, 1982; Koyama,1985; Soerjani et al., 1987; Moody, 1989; Simpson & Koyama, 1998; Simpson & Inglis, 2001	P	aquatic biotypes, crops, rice fields	AFR, ASI, AUS, IND, NA, PI, SA
Eleocharis albida Torr.	Carter, 2005	P	disturbed saltmarsh, ditches	CAR, NA
Eleocharis atropurpurea (Retz.) Kunth	Kern, 1974; Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	A	aquatic biotypes, crops, rice fields	AFR, ASI, AUS, EUR, IND, NA, PI, SA
Eleocharis attenuata (Franch. & Sav.) Palla	Holm et al.,1979; Moody, 1989	P/A?	rice fields	ASI
Eleocharis baldwinii (Torr.) Chapm.	WSSA, 1989	A	wet places	NA
Eleocharis cellulosa Torr.	Holm et al.,1979; WSSA,1989	P	brackish wet places	CA, NA, SA
Eleocharis complanata Boeckeler	Johnson, 1997	P	rice fields	AFR
Eleocharis congesta D. Don	Lin, 1968; Kern, 1974; Holm et al., 1979; Koyama, 1985; Soerjani et al., 1987; Moody, 1989; Kukkonen, 2001; Simpson & Inglis, 2001	A/P	rice fields	ASI, IND
Eleocharis dulcis Trin. ex Hensch.	Lin, 1968; Reed, 1977; Holm et al., 1979, 1997; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	P	aquatic biotypes, crops, fallow fields, rice fields	AFR, ASI, AUS, CAR, IND, NA, PI
Eleocharis elegans (Kunth) Roem. & Schult.	Kühn, 1982; Lorenzi, 1982; Kissman, 1997; Simpson & Inglis, 2001	P	aquatic biotypes, crops, rice fields	CAR, NA, PI, SA

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Eleocharis equisetina J. Presl & C. Presl	Holm et al., 1979	P		ASI, AUS, PI
"*Eleocharis erecta* Schumac."	Holm et al., 1979			AFR
Eleocharis filiculmis Kunth	Reed, 1977; Kühn, 1982; Lorenzi, 1982	P	aquatic, wet places	AFR, NA, SA
Eleocharis flavescens (Poir.) Urb. var. *flavescens*	Holm et al., 1979; Walters, 1980	A/P	rice fields	CAR, EUR, NA, SA
Eleocharis flavescens var. *olivacea* (Torr.) Gleason	Walters, 1980	A/P	rice fields	EUR, NA
Eleocharis geniculata (L.) Roem. & Schult.	Cardenas et al., 1972; Kern, 1974; Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Wagner et al., 1990; Kissman, 1997; Waterhouse, 1997; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	A	aquatic biotypes, crops, grasslands, moist areas, rice fields, taro paddies	AFR, ASI, AUS, EUR, IND, NA, PI, SA
Eleocharis interstincta (Vahl) Roem. & Schult.	Holm et al., 1979	P		NA, SA
Eleocharis kuroguwai Ohwi	Holm et al., 1979	P		ASI
Eleocharis macbarronii K. L. Wilson	Wilson, 1993	P	rice fields	AUS
Eleocharis macrostachya Britton		P		NA
Eleocharis mamillata H. Lindb.	Holm et al., 1979	P		ASI
Eleocharis montana (Kunth) Roem. & Schult.	Holm et al., 1979	P	disturbed sites, wet ditches	CAR, NA, SA
Eleocharis montevidensis Kunth	Carter, 2005	P	crops, wet ditches	NA, SA
Eleocharis multicaulis Sm.	Holm et al., 1979			EUR
Eleocharis mutata (L.) Roem. & Schult.	Holm et al., 1979; Simpson & Inglis, 2001	P	rice fields	SA
Eleocharis obtusa (Willd.) Schult.	Holm et al., 1979; Walters, 1980; Moody, 1989; WSSA, 1989; Carter, 2005	A(P)	crops, rice fields, wet places	EUR, NA, PI (Hawaii)
Eleocharis ochrostachys Steud.	Soerjani et al., 1987; Moody, 1989	P	rice fields	ASI
Eleocharis ovata (Roth) Roem. & Schult.	Holm et al., 1979	A(P)	crops, wet places	ASI, EUR, NA
Eleocharis palustris (L.) Roem. & Schult.	Holm et al., 1979, 1997; Kühn, 1982; Moody, 1989; WSSA, 1989; Simpson & Inglis, 2001	P	aquatic biotypes, rice fields	AFR, ASI, CAR, EUR, IND, NA, SA
Eleocharis parodii Barros	Wilson, 1993	P	rice fields	AUS
Eleocharis parvula (Roem. & Schult.) Link ex Bluff, Nees & Schauer	Holm et al., 1979; WSSA, 1989; Carter, 2005	P		AFR, ASI, EUR, NA, SA
Eleocharis pellucida J. Presl & C. Presl	Reed, 1977; Kühn, 1982; Zhirong et al., 1990	A/P	aquatic biotypes, crops	ASI, IND, PI
Eleocharis philippinensis Svenson	Kern, 1974; Soerjani et al., 1987; Moody, 1989; Simpson & Koyama, 1998; Simpson & Inglis, 2001	P	rice fields	ASI, AUS, PI

Appendix 2. Continued.

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Eleocharis plantaginoidea W. F. Wight	Holm et al., 1979			IND
Eleocharis quadrangulata (Michx.) Roem. & Schult.	Elliott, 1821; Holm et al., 1979; WSSA, 1989; Carter, 2005	P	pond shores, rice fields	NA
Eleocharis quinqueflora (Hartmann) O. Schwarz	Moody, 1989	P	rice fields	IND
Eleocharis radicans (Poir.) Kunth	Wagner et al., 1990	P	taro paddies	CAR, NA, PI (Hawaii), SA
Eleocharis retroflexa (Poir.) Urb.	Kern, 1974; Holm et al., 1979; Soerjani et al., 1987; Moody, 1989; Simpson & Koyama, 1998; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	A	rice fields	ASI, AUS, IND, SA
Eleocharis rostellata Torr.	WSSA, 1989	P	wet places	CAR, NA
Eleocharis sellowiana Kunth	Kissman, 1997			SA
Eleocharis sphacelata R. Br.	Holm et al., 1979	P		AUS
Eleocharis spiralis R. Br.	Moody, 1989	P	rice fields	ASI, IND
Eleocharis subtilis Boeckeler	Holm et al., 1979			CAR
Eleocharis tetraquetra Nees	Holm et al., 1979; Moody, 1989; Zhirong et al., 1990	P	rice fields	ASI, IND
Eleocharis tuberosa Schult.	Holm et al., 1979			ASI
Eleocharis valleculosa Ohwi f. *setosa* (Ohwi) Kitag.	Zhirong et al., 1990	P	rice fields, wetlands	ASI
Eleocharis variegata (Poir.) C. Presl	Holm et al., 1979; Moody, 1989			ASI
Eleocharis vivipara Link	WSSA, 1989	P	wet places	NA
Eleocharis wichurae Boeckeler	Reed, 1977	P?	wet places	ASI
Eleocharis wolfii A. Gray	Holm et al., 1979; Moody, 1989	P	rice fields, wet places	ASI, NA
Eleocharis yokoscensis (Franch. & Sav.) Ts. Tang & F. T. Wang	Zhirong et al., 1990	P	rice fields, wetlands	ASI
Fimbristylis acuminata Vahl	Kern, 1974; Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	P	aquatic biotypes, crops, rice fields	ASI, AUS, IND, PI
Fimbristylis aestivalis (Retz.) Vahl	Lin, 1968; Kern, 1974; Reed, 1977; Holm et al., 1979; Kühn, 1982; Koyama, 1985; Soerjani et al., 1987; Moody, 1989; Zhirong et al., 1990; Wagner et al., 1990; Simpson & Koyama, 1998; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	A	aquatic biotypes, crops, rice fields, taro paddies	ASI, AUS, IND, PI, SA
Fimbristylis albicans Nees	Moody, 1989		rice fields	IND

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Fimbristylis alboviridis C. B. Clarke	Soerjani et al., 1987; Moody, 1989		rice fields	ASI, IND
Fimbristylis anisoclada Ohwi	Kern, 1974; Moody, 1989	P	rice fields	ASI, IND, PI
Fimbristylis annua (All.) Roem. & Schult.	Kral, 1971; Cardenas et al., 1972; Godfrey & Wooten, 1979; Holm et al., 1979; Moody, 1989; WSSA, 1989; DeFelice & Bryson, 2004; Carter, 2005	A	rice fields	ASI, EUR, NA, PI, SA
Fimbristylis argentea (Rottb.) Vahl	Moody, 1989; Ravi & Mohanan, 2002	P	rice fields	ASI, IND
Fimbristylis autumnalis (L.) Roem. & Schult.	Holm et al., 1979; Lorenzi, 1982; Kühn, 1982; WSSA, 1989; Kissman, 1997; Simpson & Inglis, 2001	A	aquatic biotypes, crops, rice fields	AFR, ASI, IND, NA, SA
Fimbristylis bisumbellata (Forssk.) Bubani	Kern, 1974; Holm et al., 1979; DeFilipps, 1980b; Koyama, 1985; Soerjani et al., 1987; Moody, 1989; Simpson & Koyama, 1998; Kukkonen, 2001	A	cultivated fields, rice fields	AFR, AUS, EUR, IND, PI
Fimbristylis caesia Miq.	Kern, 1974; Moody, 1989	A?	edges of rice fields, roadsides	PI
Fimbristylis caroliniana (Lam.) Fernald	Kral, 1971	P	disturbed soil, waste lands	CAR, NA
Fimbristylis castanea (Michx.) Vahl	Kral, 1971	P	disturbed soil, waste lands	CAR, NA
Fimbristylis cinnamometorum (Vahl) Kunth	Moody, 1989	A/P	rice fields	IND
Fimbristylis complanata (Retz.) Link	Kern, 1974; Holm et al., 1979; Moody, 1989; Simpson & Koyama, 1998; Simpson & Inglis, 2001	P	aquatic biotypes, crops, rice fields	ASI, IND, PI
Fimbristylis cymosa R. Br.	Holm et al., 1979; Moody, 1989; Waterhouse, 1997	P	rice fields, sweet potato, taro	ASI, PI
Fimbristylis decipiens Kral	Kral, 1971; Godfrey & Wooten, 1979	A	disturbed soil, waste lands	NA
Fimbristylis dichotoma (L.) Vahl	Lin, 1968; Kral, 1971; Kern, 1974; Holm et al., 1977, 1979; Godfrey & Wooten, 1979; Kühn, 1982; Lorenzi, 1982; Koyama, 1985; Soerjani et al., 1987; Moody, 1989; WSSA, 1989; Zhirong et al., 1990; Gordon-Gray, 1995; Kissman, 1997; Waterhouse, 1997; Simpson & Koyama, 1998; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002; Carter, 2005	A/P	aquatic biotypes, crops, grasslands, lawns, rice fields, sugarcane and tea plantations, waste places, wetlands	AFR, ASI, AUS, EUR, IND, NA, PI, SA
Fimbristylis dipsacea (Rottb.) C. B. Clarke	Kern, 1974; Moody, 1989; Ravi & Mohanan, 2002	A	rice fields	AFR, ASI, PI
Fimbristylis dura (Zoll. & Moritz) Merr.	Kern, 1974; Moody, 1989	P	rice fields	ASI, IND, PI

Appendix 2. Continued.

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Fimbristylis eragrostis (Nees) Hance	Moody, 1989	P	rice fields	ASI
Fimbristylis falcata (Vahl) Kunth	Moody, 1989	P	rice fields	IND
Fimbristylis ferruginea (L.) Vahl	Reed,1977; Holm et al.,1979; Kühn, 1982; Akobundu & Agyakwa, 1987; Moody, 1989; Johnson, 1997; Simpson & Inglis, 2001	A/P	aquatic biotypes, rice fields, waste places	ASI, AUS, EUR, IND, PI, SA
Fimbristylis globulosa (Retz.) Kunth	Kern, 1974; Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; Simpson & Koyama, 1998; Simpson & Inglis, 2001	P	aquatic biotypes, crops, rice fields	ASI, IND, PI
Fimbristylis griffithii Boeckeler	Soerjani et al., 1987; Moody, 1989	A	rice fields	ASI
Fimbristylis hispidula (Vahl) Kunth	Kühn, 1982	A/P	aquatic biotypes, crops, grasslands	ASI, NA, PI, SA
Fimbristylis koidzumiana Ohwi	Lin, 1968; Reed, 1977; Holm et al., 1979	A	crops, wet places	ASI
Fimbristylis littoralis Gaudich.	Kern, 1974; Moody, 1981, 1989; Akobundu & Agyakwa, 1987; Johnson, 1997	A/P	rice fields	pantropical
Fimbristylis merrillii J. Kern	Kern, 1974; Moody, 1989	A	rice fields	ASI, AUS, PI
Fimbristylis miliacea (L.) Vahl	Ohwi, 1965; Lin, 1968; Kral, 1971; Kern, 1974; Reed, 1977; Holm et al., 1977, 1979; Kühn, 1982; Lorenzi, 1982; Koyama, 1985; Soerjani et al., 1987; Moody, 1989; WSSA, 1989; Zhirong et al., 1990; Kissman,1997; Waterhouse, 1997; Simpson & Koyama, 1998; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002; DeFelice & Bryson, 2004; Carter, 2005	A/B	aquatic biotypes, crops, rice fields, wet places	AFR, ASI, AUS, CAR, IND, NA, PI, SA
Fimbristylis nutans (Retz.) Vahl	Moody, 1989; Simpson & Koyama, 1998; Simpson & Inglis, 2001	P	rice fields	ASI, AUS, IND
Fimbristylis pauciflora R. Br.	Moody, 1989; Wilson, 1993; Simpson & Inglis, 2001	P/A?	rice fields	ASI, AUS, IND, PI
Fimbristylis polytrichoides (Retz.) R. Br.	Moody, 1989	P	rice fields	AFR, AUS, IND
Fimbristylis quinquangularis (Vahl) Kunth	Holm et al., 1979; Koyama, 1985; Moody, 1989; Kukkonen, 2001	A/B	rice fields	AFR, ASI, IND
Fimbristylis schoenoides (Retz.) Vahl	Kern, 1974; Holm et al., 1979; Koyama, 1985; Soerjani et al., 1987; Moody, 1989; Simpson & Koyama, 1998; Simpson & Inglis, 2001; Carter, 2005	A/P	rice fields	ASI, AUS, IND, NA

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Fimbristylis sericea R. Br.	Moody, 1989		rice fields	ASI, AUS, IND
Fimbristylis squarrosa Vahl	Holm et al., 1979; Moody, 1989; Kukkonen, 2001	A	rice fields	AFR, ASI, EUR, IND, SA
Fimbristylis stauntoni Debeaux & Franch.	Zhirong et al., 1990	A	rice fields, wetlands	ASI
Fimbristylis stolonifera C. B. Clarke	Moody, 1989		rice fields	ASI
Fimbristylis subbispicata Nees & Meyen	Holm et al., 1979; Moody, 1989		rice fields	ASI, IND
Fimbristylis tenera Roem. & Schult.	Holm et al., 1979; Moody, 1989	A/P	rice fields	IND
Fimbristylis tetragona R. Br.	Kern, 1974; Holm et al., 1979; Koyama, 1985; Moody, 1989	P	rice fields	ASI, AUS, IND, PI
Fimbristylis thonningiana Boeckeler	Holm et al., 1979			AFR
Fimbristylis tomentosa Vahl	Kern, 1974; Soerjani et al., 1987; Moody, 1989; Carter, 2005	A	rice fields	AFR, ASI, AUS, NA, PI
Fimbristylis tristachya R. Br.	Holm et al., 1979; Moody, 1989		rice fields	AFR, ASI
Fimbristylis turkestanica (Regel) B. Fedtsch.	Kukkonen, 2001	P	fields, gardens	AFR, ASI, EUR, IND
Fimbristylis verrucifera (Maxim.) Makino	Reed, 1977	A	wet places	ASI
Fuirena breviseta (Coville) Coville	WSSA, 1989	P		NA
Fuirena ciliaris (L.) Roxb.	Ohwi, 1965; Kern, 1974; Holm et al., 1979; Kühn, 1982; Akobundu & Agyakwa, 1987; Soerjani et al., 1987; Moody, 1989; Simpson & Koyama, 1998; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	A	aquatic biotypes, crops, grasslands, rice fields	AFR, ASI, AUS, IND, PI
Fuirena pumila (Torr.) Spreng.	WSSA, 1989	A		NA
Fuirena scirpoidea Michx.	WSSA, 1989	P		NA
Fuirena simplex Vahl	WSSA, 1989	A/P		NA
Fuirena squarrosa Michx.	WSSA, 1989	P		NA
Fuirena stricta Steud. subsp. *chlorocarpa* (Ridl.) Lye	Johnson, 1997; Simpson & Inglis, 2001	P	rice fields	AFR
Fuirena umbellata Rottb.	Kern, 1974; Holm et al., 1979; Kühn, 1982; Akobundu & Agyakwa, 1987; Soerjani et al., 1987; Moody, 1989; Johnson, 1997; Ravi & Mohanan, 2002	P	aquatic biotypes, ditches, grasslands, rice fields	AFR, ASI, AUS, IND, PI, SA
Isolepis carinata Hook. & Arn. ex Torr.	Godfrey & Wooten, 1979; WSSA, 1989	A	crops, grasslands, waste places	NA
Kyllinga aurata Nees	Holm et al., 1979	P		AFR

Appendix 2. Continued.

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Kyllinga brevifolia Rottb.	Lin, 1968; Cardenas et al., 1972; Kern, 1974; Godfrey & Wooten, 1979; Kühn, 1982; Lorenzi, 1982; Koyama, 1985; Soerjani et al., 1987; WSSA, 1989; Zhirong et al., 1990; Wagner et al., 1990; Wilson, 1993; Gordon-Gray, 1995; Holm et al., 1997; Kissman, 1997; Waterhouse, 1997; Bryson et al., 1998; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002; Carter, 2005	P	crops, disturbed sites, fallow fields, gardens, grasslands, pastures, rice fields, turf, waste places	AFR, ASI, AUS, CAR, EUR, IND, NA, PI, SA
Kyllinga bulbosa P. Beauv.	Akobundu & Agyakwa, 1987	P	rice fields	AFR
Kyllinga colorata (L.) Druce	Zhirong et al., 1990	P		ASI
Kyllinga erecta Schumach.	Terry, 1976; Holm et al., 1979; Kühn, 1982; Akobundu & Agyakwa, 1987; Gordon-Gray, 1995; Johnson, 1997; Simpson & Inglis, 2001	P	crops, cultivated lands, grasslands, rice fields, waste places	AFR, ASI, IND, PI
Kyllinga gracillima Miq.	WSSA, 1989; Bryson et al., 1998; Simpson & Inglis, 2001	P	crops, grasslands, turf, waste places	ASI, NA
Kyllinga melanosperma Nees	Moody, 1989	P	rice fields	IND, PI
Kyllinga nemoralis (J. R. Forst. & G. Forst.) Dandy ex Hutch. & Dalziel	Holm et al., 1979; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; WSSA, 1989; Wagner et al., 1990; Waterhouse, 1997; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	P	crops, gardens, grasslands, lawns, pastures, plantations, rice fields, roadsides, turf, waste places	AFR, ASI, AUS, IND, PI, SA
Kyllinga odorata Vahl	Terry, 1976; Godfrey & Wooten, 1979; Holm et al., 1979; Lorenzi, 1982; Moody, 1989; Wilson, 1993; Gordon-Gray, 1995; Kissman, 1997; Bryson et al., 1998; Simpson & Inglis, 2001; Carter, 2005	P	damp sandy ground, disturbed grassland, gardens, pastures, lawns, rice fields, turf, waste places	AFR, ASI, AUS, NA, PI, SA
Kyllinga polyphylla Willd. ex Kunth	Holm et al., 1979; Moody, 1989; Waterhouse, 1997; Simpson & Inglis, 2001	P	agricultural land, crops, pastures, rice fields, roadsides, turf, waste places	AFR, ASI, PI
Kyllinga pumila Michx.	Holm et al., 1979; Akobundu & Agyakwa, 1987; WSSA, 1989; Le Bourgeois & Merlier, 1995; Johnson, 1997; Bryson et al., 1998; Simpson & Inglis, 2001	A	crops, pastures, turf, rice fields, waste places	AFR, CAR, NA, SA

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Kyllinga squamulata Thonn. ex Vahl	Terry, 1976; Akobundu & Agyakwa, 1987; WSSA, 1989; Le Bourgeois & Merlier, 1995; Bryson et al., 1998; Simpson & Inglis, 2001; Carter, 2005	A	cultivated lands, turf, waste places	AFR, ASI, CAR, IND, NA
Kyllinga triceps Rottb.	Kern, 1974; Moody, 1989; Le Bourgeois & Merlier, 1995; Simpson & Inglis, 2001	P	sandy lawn	AFR, ASI, AUS, IND, PI
Lepidosperma chinense Nees & Meyen	Kern, 1974	P	rice fields	ASI, PI
Lepironia articulata (Retz.) Domin	Moody, 1989	P	rice fields	ASI
Lipocarpha chinensis (Osbeck) J. Kern	Lin, 1968; Kern, 1974; Reed, 1977; Holm et al., 1979; Kühn, 1982; Koyama, 1985; Soerjani et al., 1987; Johnson, 1997; Simpson & Inglis, 2001	A/P	aquatic biotypes, crops, grasslands, rice fields, waste wet places	AFR, ASI, AUS, IND
Lipocarpha maculata (Michx.) Torr.	Carter, pers. obs.	A	disturbed wet sites, ditches roadsides	NA, SA
Lipocarpha microcephala (R. Br.) Kunth	Kern, 1974; Holm et al., 1979	A	rice fields, sugarcane fields	ASI, AUS, IND
Lipocarpha squarrosa (L.) Goetgh.	Kern, 1974; Moody 1989; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	A/P?	crops, cultivated land, rice fields, wet fields	AFR, ASI, AUS, IND
Mapania cuspidata (Miq.) Uittien	Moody, 1989	P	rice fields	ASI
Oxycaryum cubense (Poepp. & Kunth) Palla	Holm et al., 1979; Simpson & Inglis, 2001	P	aquatic, floating mats	AFR, CAR, NA, SA
Rhynchospora aurea Vahl	Kissman, 1997	P		SA
Rhynchospora caduca Elliott	Wagner et al., 1990; Wagner & Herbst, 1995	P	pastures	NA, PI (Hawaii)
Rhynchospora cephalotes (L.) Vahl	Kissman, 1997	P		SA
Rhynchospora colorata (L.) H. Pfeiff.	WSSA, 1989	P	wet places	NA
Rhynchospora corniculata (Lam.) A. Gray	WSSA, 1989; DeFelice & Bryson, 2004	P	ditches, wet places	NA
Rhynchospora corymbosa (L.) Britton	Kern, 1974; Holm et al., 1979; Kühn, 1982; Lorenzi, 1982; Koyama, 1985; Akobundu & Agyakwa, 1987; Soerjani et al., 1987; Moody, 1989; Johnson, 1997; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	P	aquatic biotypes, crops, rice fields, waste places, wet places	AFR, ASI, AUS, IND, PI, SA
Rhynchospora fascicularis (Michx.) Vahl	Godfrey & Wooten, 1979	P	pastures, roadsides	CAR, NA, SA
Rhynchospora globularis (Chapm.) Small	Godfrey & Wooten, 1979; WSSA, 1989	P	disturbed areas, roadsides	CAR, NA, PI (Hawaii), SA
Rhynchospora glomerata (L.) Vahl	Godfrey & Wooten, 1979	P	pastures, roadsides	NA

Appendix 2. Continued.

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Rhynchospora holoschoenoides (Rich.) Herter	Simpson & Inglis, 2001	P	rice fields	AFR, SA
Rhynchospora inexpansa (Michx.) Vahl	Godfrey & Wooten, 1979	P	pastures, roadsides	NA
Rhynchospora latifolia (Baldwin) W. W. Thomas	WSSA, 1989	P	wet places	NA
Rhynchospora longisetis R. Br.	Moody, 1989	A	rice fields	ASI
Rhynchospora microcarpa Baldwin ex A.Gray	Godfrey & Wooten, 1979	P	pastures, roadsides	CAR, NA
Rhynchospora nervosa (Vahl) Boeckeler	Cardenas et al., 1972; Reed, 1977; Kühn, 1982; Lorenzi, 1982; Kissman, 1997; Simpson & Inglis, 2001	P	crops, grasslands, low elevations, wet places	CAR, NA, SA
Rhynchospora radicans H. Pfeiff. subsp. *microcephala* (Bertero ex Spreng.) W. W. Thomas	Strong & Wagner, 1997	A/P	cultivated lands	CAR, PI (Hawaii), SA
Rhynchospora rubra (Lour.) Makino	Holm et al., 1979; Moody, 1989	A/P	rice fields	ASI
Rhynchospora submarginata Kük.	Kern, 1974; Moody, 1989	A	rice fields	ASI, AUS, IND, PI
Rhynchospora tenuis Link	Holm et al., 1979			SA
Rhynchospora wightiana (Nees) Steud.	Kern, 1974; Moody, 1989	A	fallow rice fields, rice fields	ASI, IND, PI
Schoenoplectus acutus (Muhl. ex J. M. Bigelow) Á. Löve & D. Löve	USDA, 1970; Holm et al., 1979; Kühn, 1982; Moody, 1989; WSSA, 1989; DeFelice & Bryson, 2004	P	aquatic biotypes	ASI, NA
Schoenoplectus americanus (Pers.) Volkart ex Schinz & R. Keller	Holm et al., 1979; WSSA, 1989	P		NA
Schoenoplectus articulatus (L.) Palla	Kern, 1974; Holm et al., 1979; Soerjani et al., 1987; Moody, 1989; Simpson & Koyama, 1998; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	A/P	rice fields, swampy fallow fields	AFR, ASI, AUS
Schoenoplectus californicus (C. A. Mey.) Soják	Holm et al., 1979; WSSA, 1989; Kissman, 1997	P	wet places	NA, PI, SA
Schoenoplectus corymbosus (Roth ex Roem. & Schult.) J. Raynal	Moody, 1989	P	rice fields	IND
Schoenoplectus erectus (Poir.) Palla ex J. Raynal	Holm et al., 1979; Kühn, 1982	A	aquatic biotypes, wet places	AFR, ASI, AUS, EUR, IND, NA, PI, SA
Schoenoplectus grossus (L. f.) Palla	Kern, 1974; Holm et al., 1979, 1997; Soerjani et al., 1987; Moody, 1989	P	ditches, rice fields	ASI, AUS, PI

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Schoenoplectus juncoides (Roxb.) Palla	Lin, 1968; Kern, 1974; Holm et al., 1979; DeFilipps, 1980a; Koyama, 1985; Soerjani et al., 1987; Moody, 1989; Zhirong et al., 1990; Simpson & Koyama, 1998; Kukkonen, 2001; Simpson & Inglis, 2001	A	aquatic biotypes, crops, rice fields	AFR, ASI, EUR, IND, PI
Schoenoplectus lacustris (L.) Palla	Holm et al., 1979; Moody, 1989; Simpson & Inglis, 2001	P	aquatic biotypes	AFR, ASI, EUR, PI
Schoenoplectus lacustris (L.) Palla × *S. triqueter* (L.) Palla	Kukkonen, 2001	P	rice fields	ASI, IND
Schoenoplectus lateriflorus (J. F. Gmel.) Lye	Kern, 1974; Soerjani et al., 1987; Moody, 1989; Kukkonen, 2001	A	rice fields	ASI, AUS, IND
Schoenoplectus litoralis (Schrad.) Palla	Holm et al., 1979; Kühn, 1982; Simpson & Inglis, 2001	P	aquatic biotypes	AFR, ASI, AUS, EUR, IND, PI
Schoenoplectus mucronatus (L.) Palla	Kern, 1974; Reed, 1977; Holm et al., 1979, 1997; Kühn, 1982; Soerjani et al., 1987; Moody, 1989; WSSA, 1989; Simpson & Koyama, 1998; Kukkonen, 2001; Simpson & Inglis, 2001; DeFelice & Bryson, 2004	P	aquatic biotypes, ditches, rice fields, wet places	AFR, ASI, AUS, EUR, IND, NA, PI
Schoenoplectus pungens (Vahl) Palla	Moore & Edgar, 1970; Simpson & Inglis, 2001	P	aquatic, unspecified	AUS, CAR, EUR, NA, PI, SA
Schoenoplectus roylei (Nees) Ovcz. & Czukav.	Moody, 1989; Kukkonen, 2001; Simpson & Inglis, 2001	A	ditches, rice fields	AFR, IND
Schoenoplectus senegalensis (Hochst. ex Steud.) Palla ex J. Raynal	Akobundu & Agyakwa, 1987; Johnson, 1997	A	rice fields	AFR
Schoenoplectus supinus (L.) Palla	Moody, 1989; Simpson & Koyama, 1998; Kukkonen, 2001; Simpson & Inglis, 2001; Ravi & Mohanan, 2002	A	rice fields	ASI, AUS, IND
Schoenoplectus tabernaemontani (C. C. Gmel.) Palla	Reed, 1977; WSSA, 1989; Zhirong et al., 1990	P	aquatic, brackish water	AFR, ASI, AUS, EUR, IND, NA
Schoenoplectus triqueter (L.) Palla	Reed, 1977; Holm et al., 1979; Kühn, 1982; Moody, 1989; Zhirong et al., 1990; Kukkonen, 2001; Simpson & Inglis, 2001	P	aquatic biotypes, rice fields	AFR, ASI, EUR, IND, PI
Schoenoplectus wallichii (Nees) T. Koyama	Lin, 1968; Kern, 1974; Reed, 1977; Holm et al., 1979; Moody, 1989	P	rice fields, wet places	ASI, IND
Scirpodendron ghaeri (Gaertn.) Merr.	Moody, 1989	P	rice fields	ASI
Scirpus atrovirens Willd.	Holm et al., 1979; WSSA, 1989	P	roadsides, wet places	NA
Scirpus cyperinus (L.) Kunth	Holm et al., 1979; WSSA, 1989; Carter, 2005	P	roadsides, wet places	NA

Appendix 2. Continued.

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Scirpus giganteus Kunth	Kissman, 1997	P		SA
Scirpus holoschoenus L.	Reed, 1977; Holm et al., 1979; Kühn, 1982	P	crops, waste places	AFR, ASI, EUR, IND
Scirpus michelianus L.	Moody, 1989; Zhirong et al., 1990	A	farmland, field borders, rice fields	ASI, IND
Scirpus pendulus Muhl.	Holm et al., 1979	P	roadsides, wet places	AUS, NA
Scirpus sylvaticus L.	Holm et al., 1979	P		EUR
Scirpus triangulatus Roxb.	Holm et al., 1979	P		AUS
Scleria bancana Miq.	Holm et al., 1979; Moody, 1989		rice fields	ASI
Scleria biflora Roxb.	Kern, 1974; Koyama, 1985; Moody, 1989	A	rice fields, roadsides, tea plantations	ASI, IND, PI
Scleria boivinii Steud.	Holm et al., 1979			AFR
Scleria bracteata Cav.	Holm et al., 1979; Kissman, 1997			SA
Scleria canescens Boeckeler	Holm et al., 1979			NA, SA
Scleria caricina (R. Br.) Benth.	Simpson & Koyama, 1998; Simpson & Inglis, 2001		rice fields	PI
Scleria depressa (C. B. Clarke) Nelmes	Johnson, 1997	P	rice fields	AFR
Scleria lacustris C. Wright	Tobe et al.,1998; Wunderlin, 1998; Jacono, 2001	A	aquatic waste places, wet places	AFR, CAR, NA, SA
Scleria laevis Retz.	Kern, 1974; Holm et al., 1979; Moody, 1989; Ravi & Mohanan, 2002	P	fallow rice fields	ASI, AUS, IND, PI
Scleria lithosperma (L.) Sw.	Holm et al., 1979; Kühn, 1982; Moody, 1989; Simpson & Inglis, 2001	P	aquatic biotypes, crops, rice fields, waste places, wet places	AFR, ASI, IND, PI, SA
Scleria melaleuca Rchb. ex Schltdl. & Cham.	Cardenas et al., 1972; Holm et al., 1979; Lorenzi, 1982; Moody, 1989	P		CAR, SA
Scleria myriocarpa Steud.	Holm et al., 1979			SA
Scleria naumanniana Boeckeler	Akobundu & Agyakwa, 1987	P	forest clearings, wet areas	AFR
Scleria novae-hollandiae Boeckeler	Kern, 1974; Moody, 1989	A	fallow rice fields, rice fields	AUS, IND, PI
Scleria oblata S. T. Blake	Holm et al., 1979; Moody, 1989	P	rice fields	ASI
Scleria poaeformis Retz.	Holm et al., 1979; Moody, 1989	P	rice fields	ASI, AUS, IND
Scleria polycarpa Boeckeler	Holm et al., 1979	P		PI
Scleria purpurascens Steud.	Holm et al., 1979; Moody, 1989	P	rice fields	ASI

Species[1]	Source	Habit[2]	Habitat	Distribution[3]
Scleria rugosa R. Br.	Kern, 1974; Koyama, 1985; Moody, 1989	A	rice fields	ASI, AUS, IND, PI
Scleria scindens Nees	Reed, 1977	P		CAR
Scleria scrobiculata Nees & Meyen	Holm et al., 1979; Moody, 1989	P	rice fields	PI
Scleria sumatrensis Retz.	Holm et al., 1979; Kühn, 1982; Moody, 1989; Simpson & Inglis, 2001	A	aquatic biotypes, crops, forests, rice fields	ASI, AUS, IND, PI
Scleria tessellata Willd. var. *sphaerocarpa* E. A. Rob.	Kühn, 1982; Moody, 1989; Le Bourgeois & Merlier, 1995; Simpson & Inglis, 2001	A	aquatic biotypes, grasslands, rice fields, wet places	AFR, ASI, AUS, IND, PI, SA
Scleria verrucosa Willd.	Akobundu & Agyakwa, 1987	P	wet areas	AFR

[1] Plant nomenclature follows *Flora of North America*, volume 23; plant names were also verified through the Missouri Botanical Garden w[3]TROPICOS VAST database (rev. 1.5) (http://mobot.mobot.org/W3T/Search/vast.html) and the International Plant Names Index (http://www.ipni.org/index.html). A more inclusive list of names cited in the references is available from the authors.

[2] A = annual; B = biennial; P = perennial; supplemental data from Kükenthal (1935–1936), Kern (1974), Holm et al. (1977, 1997), Haines and Lye (1983), Koyama (1985), Soerjani et al. (1987), Wilson (1993), Gordon-Gray (1995), Lye (1995), Simpson and Inglis (2001), Kukkonen (2001), and *Flora of North America*, volume 23.

[3] AFR = Africa including Madagascar; ASI = Asia; AUS = Australia; CAR = Caribbean Islands; EUR = Europe; IND = Indian subcontinent including Sri Lanka; NA = North America; PI = Pacific Islands; SA = South America.

Chapter 3

Diversity, Endemism, and Phytogeography of North American Coastal Plain Sedges

Bruce A. Sorrie

ABSTRACT The North American Coastal Plain extends from southeastern Massachusetts to northern Veracruz, Mexico, and extends northward via the Mississippi Embayment to southern Illinois. The area covers 1,166,000 sq. km, or about 8% of the North American land mass. The physiographic Coastal Plain is nearly conterminous with the Coastal Plain Floristic Province, a distinct area marked by a sharp geological and floristic boundary and noted for high species diversity: of the 19,400 plant taxa native to North America, 6091 (31.4%) occur on the Coastal Plain. Sedges of the Coastal Plain are similarly diverse: 22 genera, 490 native species and infraspecific taxa, and 40 alien taxa. The total of 530 full species and infraspecific taxa compares favorably with the total of 478 within the Gray's Manual range, an area twice the size of the Coastal Plain and one considered to be especially rich in sedges. Endemism is high in Coastal Plain sedges, with 127 taxa (25.9%), and parallels the rate of endemism for the entire Coastal Plain flora (26.8%). Within North America, only the Californian Floristic Province and the Mexican Highlands Floristic Province exceed this rate of endemism. The Coastal Plain has drawn its Cyperaceae from disparate regions: boreal, Appalachian, Neotropical, prairie, and maritime. An analysis of the distributions of endemic sedge taxa suggests the existence of at least 13 phytogeographic patterns. In each of these patterns, multiple taxa occupy essentially the same range. These patterns include micro-endemics that are restricted to a few counties to very wide-ranging taxa. Several patterns are notable for taxa that are disjunct to other floristic provinces.

KEY WORDS Coastal Plain, diversity, endemism, floristic province, phytogeography.

Papers or manuals treating whole floristic provinces (FP; also termed phytogeographic province) are uncommon in North American botanical literature. One notable exception is the *Intermountain Flora* (Cronquist et al., 1972, 1977, 1984, 1997; Barneby, 1989; Cronquist, 1994), which treats the Great Basin FP. Another exception is Rydberg's (1932) *Flora of the Prairies and Plains of Central North America,* which covers the North American Prairies FP. Unfortunately, its successors, *Atlas of the Flora of the Great Plains* (Great Plains Flora Association, 1977) and *Flora of the Great Plains* (Great Plains Flora Association, 1986), treat only the portion south of the Canadian border. Sorrie and Weakley (2001) discuss phytogeographic patterns within the Atlantic and Gulf Coastal Plain FP and provide a numerical summary of the province's species, infraspecific taxa, aliens, and endemics. Of the 11 floristic provinces recognized for North America by Thorne (1993), excluding the Neotropical kingdom, only the above works treat entire provinces.

Other authors treat portions of floristic provinces. Raven and Axelrod (1978) summarized the flora of California and included a numeric summary of the California FP, but theirs was not a treatise of the whole province. Shreve and Wiggins (1964) treat the Sonoran Subprovince of the Sonoran FP, and Crosswhite (1980) summarized the Tamaulipan Subprovince as it occurs in south Texas. Ricketts et al. (1999) and Stein et al. (2000) divide North American floristic provinces into smaller ecoregions as a means of prioritizing conservation efforts, but nowhere are whole floristic provinces discussed.

The reasons why so few workers in a continent with a well-known flora have treated entire floristic provinces are obscure. This situation is especially perplexing in light of the recent interest in the Earth's biodiversity and conservation of the most significant "hotspots." To make accurate and meaningful assessments of and comparisons between ecoregions and hotspots, one must have knowledge of the floristic provinces in which they occur. The concept of floristic provinces has evolved as an attempt to divide up the globe's land masses into natural units based on plant distributions, floristic similarity and dissimilarity, evolutionary relationships, major vegetation types, and degree of endemism (Takhtajan, 1986). While it may be of interest to compare the refugia of the Klamath-Siskiyou Mountains and the southern Appalachian Mountains, it is more informative to compare the floristic provinces of which each is a part: the Californian FP and the Appalachian FP.

This paper continues the examination of the Atlantic and Gulf Coastal Plain FP begun by Sorrie and Weakley (2001). Here, however, I treat a critical subset of the flora of the region, the Cyperaceae. In most floras, floristic lists, and vegetation plots of the Coastal Plain, the Cyperaceae rank among the top four families in species richness (the others being the Asteraceae, Poaceae, and Leguminosae).

Methods

The Atlantic and Gulf Coastal Plain FP has been defined by Sorrie and Weakley (2001), based on Takhtajan (1986). Figure 1 depicts the region. Numbers of Cyperaceae found within the boundaries of the Coastal Plain are derived from a complete list of vascular plants of the province (Sorrie & Weakley, in prep.). Numbers of Cyperaceae from the Gray's Manual range are derived from the table on p. lxi in Fernald (1950), updated with data from draft manuscripts for *Flora of North America* (2002) as supplied by A. A. Reznicek. Numbers of Cyperaceae from the Gleason and Cronquist range are derived from counting taxa in Gleason and Cronquist (1991). Nomenclature follows that of *Flora of North America* (2002).

Patterns of distribution are based on county-level dot maps prepared for more than 900 coastal plain endemics and near-endemics. Dot map data were derived from herbarium specimens, Natural Heritage Program databases, state floras and plant atlases (published or online), and personal communications with knowledgeable botanists.

The question of whether to include southern Florida and southern Texas within the Coastal Plain was addressed by Sorrie and Weakley (2001). From a floristic standpoint, the former lies within the West Indian FP and the latter in the Tamaulipan Subprovince of the Sonoran FP, although both occur within the geological Coastal Plain. In this paper as before, I take the broad view. However, a strict interpretation may be accommodated as follows. If southern Florida and southern Texas are excluded from the present paper, the diversity totals in Table 1 would be

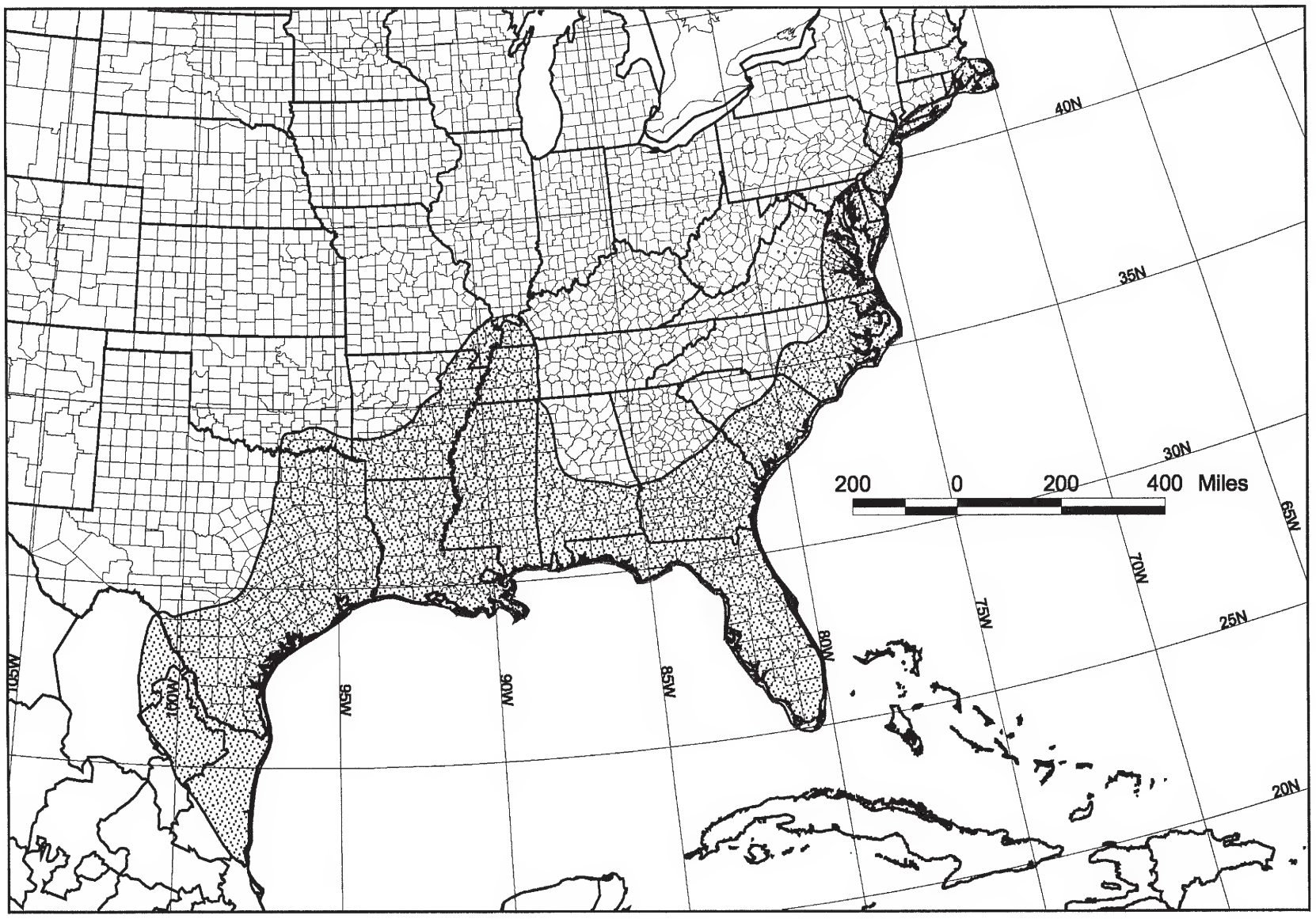

Figure 1. Coastal Plain Floristic Province.

diminished by twelve species: *Cyperus floridanus* Britton in Small, *C. fuligineus* Chapm., *C. giganteus* Vahl (alien), *C. hyalinus* Vahl (alien), *C. lentiginosus* Millsp. & Chase (alien), *C. macrocephalus* Liebm., *Eleocharis acutangula* (Roxb.) Schult., *E. brachycarpa* Svenson, *E. cylindrica* Buckley, *Rhynchospora eximia* (Nees) Boeck., *R. floridensis* (Britton ex Small) H. Pfeiff., and *Scleria lacustris* C. Wright (alien). These 12 species, a mere 2% of the Coastal Plain sedge flora, have no significant effect on the results or conclusions of this paper.

Coastal Plain Sedge Diversity

Table 1 lists the Cyperaceae of the North American Coastal Plain. Columns list numbers for native full species, native infraspecific taxa (varieties or subspecies according to authors), alien taxa, and total taxa. Twenty-two genera are represented. The total of 490 native full species and native infraspecific taxa represents 8% of the native vascular plants known from the Coastal Plain. When we include the 40 alien taxa, the total of 530 represents 6.6% of the total Coastal Plain flora. The five largest genera are *Carex* L. (216 taxa), *Cyperus* L. (84), *Rhynchospora* Vahl (74), *Eleocharis* R. Br. (51), and *Scleria* P. J. Bergius (19). *Rhynchospora*, *Cyperus*, and *Scleria* are well represented, since these are genera whose diversity is greatest within tropical and subtropical latitudes. *Carex* and *Eleocharis* are surprisingly well represented on the Coastal Plain, given that maximum global diversity of both genera is within temperate latitudes. The 40 alien taxa represent only 7.5% of the total sedge flora of the Coastal Plain and contribute substantially only within *Cyperus* (26.2%) and *Kyllinga* Rottb. (40%).

One indication of the diversity of Coastal Plain sedges is the number of unlikely taxa found there. Table 2 lists many of these unusual members of the Coastal Plain. Most are species at the periphery of their ranges (i.e., *Carex albursina* E. Sheld. and *Eriophorum vaginatum* L.), while others are disjunct (i.e., *C. crawei* Dewey and *C. exilis* Dewey) and emanate from boreal, north temperate, and prairie

Table 1. Diversity of Coastal Plain Cyperaceae. Columns represent genera, number of native species, number of native infraspecific taxa, alien taxa, and total taxa.

Genus	Native spp.	Infra	Alien	Total
Abildgaardia	1	0	0	1
Bolboschoenus (Asch.) Palla	4	0	0	4
Bulbostylis Kunth	4	1	1	6
Carex	198	8	10	216
Cladium	2	0	0	2
Cyperus	57	5	22	84
Dulichium	1	0	0	1
Eleocharis	48	2	1	51
Eriophorum	5	0	0	5
Fimbristylis Vahl	10	0	3	13
Fuirena Rottb.	7	1	0	8
Isolepis R. Br.	2	0	0	2
Kyllinga	3	0	2	5
Lipocarpha R. Br.	4	0	0	4
Oxycaryum	1	0	0	1
Remirea	1	0	0	1
Rhynchospora	64	10	0	74
Schoenoplectus (Rchb.) Palla	15	2	0	17
Schoenus	1	0	0	1
Scirpus L.	13	1	0	14
Scleria	14	4	1	19
Trichophorum	1	0	0	1
TOTALS	456	34	40	530

regions. While a few may no longer have extant populations on the Coastal Plain, they reflect the remarkable diversity of this relatively flat and featureless part of the North American continent.

A comparison of Coastal Plain sedge diversity with that of other floristic provinces may be of interest. The North American Prairies FP, not considered to be sedge-rich, supports 206 Cyperaceae (Great Plains Flora Association, 1977), a figure less than the 216 in the single genus *Carex* on the Coastal Plain. The Great Basin FP supports 126 species of Cyperaceae, 93 within the genus *Carex* (Cronquist et al., 1977). Numbers are not available for other floristic provinces in North America. The state of California, which may be considered a very rough approximation of the California FP, supports 217 species of Cyperaceae (Hickman, 1993), of which 143 are in *Carex*. Tucker's treatment of Cyperaceae for the *Generic Flora of the Southeastern United States* (1987) estimates 165 *Carex* for that region, which covers 14 states within portions of the Coastal Plain and Appalachian FPs.

Table 2. Selected Cyperaceae that are considered unusual on the Coastal Plain. The following are all documented by specimens in major herbaria.

Species	Location
Carex albursina E. Sheld.	S Maryland; S Illinois; W Tennessee
C. aurea Nutt.	Long Island, New York
C. crawei Dewey	SW Arkansas
C. davisii Schwein. & Torr.	W Kentucky; S Illinois
C. eburnea Boott in Hook.	Long Island, New York; SE Missouri
C. exilis Dewey	North Carolina Sandhills; S Alabama–S Mississippi
C. flava L.	S New Jersey
C. hitchcockiana Dewey	S Maryland; SE Arkansas
C. limosa L.	Cuttyhunk Island, Massachusetts; S New Jersey
C. livida (Wahlenb.) Willd.	S New Jersey
C. microdonta Torr. & Hook.	blackland prairies of Alabama–Mississippi; NW Florida limestone glade
C. oligosperma Michx.	Provincetown bogs, Cape Cod, Massachusetts
C. paleacea Schreb. ex Wahlenb.	Cape Cod, Massachusetts
C. prairea Dewey in A. W. Wood	Cape Cod and Nantucket Island, Massachusetts
C. trichocarpa Muhl. ex Willd.	S New Jersey
Cyperus engelmannii Steud.	W Tennessee; S Illinois
C. houghtonii Torr.	Long Island, New York
Eriophorum vaginatum L.	Provincetown bogs, Cape Cod, Massachusetts
Schoenoplectus heterochaetus (Chase) Soják	SE Missouri
Scirpus atrocinctus Fernald	SE Massachusetts
Trichophorum planifolium (Spreng.) Palla	S New Jersey; S Illinois

Perhaps more meaningful is a comparison with the adjacent Appalachian FP, which can be very roughly approximated by the Gray's Manual range (Fernald, 1950). Table 3 compares the taxa of the two regions. To make the comparison as accurate as possible, I have used generic concepts of Fernald (1950). Fernald's numbers have also been modified by A. A. Reznicek, based on draft manuscripts for *Flora of North America* (2002); this has resulted in a significant reduction in infraspecific taxa. Although smaller in area (1,166,000 sq. km), the total of 530 sedges on the Coastal Plain is considerably larger than the 478 sedges in the Gray's Manual range (3,238,000 sq. km), a region generally considered to be sedge-rich. Treating a similar but smaller range (2,300,000 sq. km), the taxonomically more conservative Gleason and Cronquist (1991) list about 400 sedge taxa. Among the 18 genera in Fernald, only *Carex*, the Appalachian endemic *Cymophyllus* Mack., and the boreal *Eriophorum* L. and *Kobresia* Willd. exceed corresponding numbers in genera on the Coastal Plain. In summary, the Coastal Plain FP appears to possess the richest sedge flora of any floristic province in North America. On a global scale, its 530 taxa represent 14.8% of the 3600 Cyperaceae taxa estimated for the world by Tucker (1987) or 10.6% of the 5000 estimated for the world by *Flora of North America* (2002).

Table 3. Comparison of Coastal Plain Cyperaceae with those found in Gray's Manual range. Taxa include species, subspecies, and varieties. To facilitate comparison, genera conform to those recognized by Fernald (1950). The area of the Coastal Plain is 1,166,000 sq. km; Gray's Manual range is 3,238,000 sq. km.

Genus	Taxa in Gray's	Taxa on CP
Abildgaardia	0	1
Bulbostylis	3	6
Carex	285	216
Cladium	2	2
Cymophyllus	1	0
Cyperus s.l.	40	90
Dichromena Michx.	1	4
Dulichium	1	1
Eleocharis	43	51
Eriophorum	8	5
Fimbristylis	8	13
Fuirena	5	8
Hemicarpha Nees	3	2
Kobresia	1	0
Lipocarpha	1	2
Psilocarya Torr.	2	3
Rhynchospora	26	67
Schoenus	0	1
Scirpus s.l.	37	39
Scleria	11	19
TOTALS	478	530

Coastal Plain Sedge Endemism

Although the Coastal Plain has long been known for its endemic taxa, it is only recently that the remarkable rates of endemism within the Coastal Plain flora have been calculated (Sorrie & Weakley, 2001, in prep.). With a native flora of 6091 species and infraspecific taxa, the Coastal Plain FP has 1375 full species and 260 infraspecific taxa that are endemic or near-endemic to the region, a rate of 26.8% (Sorrie & Weakley, in prep.). Only the California FP, with 47.7% endemism (Raven & Axelrod, 1978), and the Mexican Highlands FP, with possibly 70% endemism (Rzedowski, 1993), rank higher than the Coastal Plain. The Great Basin FP appears to have a rate of endemism of about 25% according to Thorne (1993).

Table 4 lists sedge genera that have endemic taxa. Rates of endemism range from 13% to 80% and average 26.9%. Even large genera (at least 50 taxa) range from 15% to 66%. These rates suggest that the Coastal Plain has contributed disproportionately to sedge endemism within North America. Rates of endemism of Cyperaceae have not been published for other North American floristic provinces, but I estimate a maximum of five species out of 206 (2.4%) are endemic to the North American Prairies FP, only one species out of 126 (0.8%) in the Great Basin FP, and about 16 out of 217 (7.4%) in the California FP.

One genus deserves special mention: *Rhynchospora*. With 74 total taxa and 49 endemics (66.2%), the Coastal Plain FP is clearly one of the major centers of speciation for *Rhynchospora*. Thomas (1994) estimates 250 species globally; 29.6% of the world total occurs on the North American Coastal Plain and 19.6% are endemic.

Nine native genera that occur on the Coastal Plain contain no endemics: *Abildgaardia* Vahl, *Cladium* P. Browne, *Dulichium* Pers., *Eriophorum*, *Kyllinga*, *Oxycaryum* Nees, *Remirea* Aubl., *Schoenus* L., and *Trichophorum* Pers. Moreover, these genera represent a total of only 18 taxa and contribute little toward species richness.

Endemic taxa and percent endemism are likely to increase over time within the Coastal Plain, as new taxa are discovered and as new combinations and other realignments are made. For example, Naczi et al. (2002) describe seven new species of *Carex*, six of which occur on the Coastal Plain and four of which are endemic. Bridges and Orzell (2000) describe a remarkably restricted endemic, *Rhynchospora megaplumosa* E. L. Bridges & Orzell, from southern peninsula Florida. Sorrie (2000) recognized the distinctiveness of *R. leptocarpa* (Chapm. ex Britton) Small, which had been synonymized for nearly 100 years. In an analysis of North American taxonomic novelties over a 20-year span (1975–1994), Hartman and Nelson (1998) ranked the "Southeast floristic area" (not the same geographic region as the Coastal Plain FP) fourth in terms of number of vascular taxa described, with 245. The authors conclude that "Further intensive inventory work in poorly known

Table 4. Endemism in Coastal Plain Cyperaceae. Columns represent genera, total native taxa, endemic species, endemic infraspecific taxa (subspecies and varieties), and percent endemism. Nine native genera without endemic taxa are excluded from this table.

Genus	Native taxa	Endemic spp.	Endemic infra	Percent
Bolboschoenus	4	1	0	25%
Bulbostylis	5	3	1	80%
Carex	206	32	0	16%
Cyperus	62	9	0	15%
Eleocharis	50	12	0	24%
Fimbristylis	10	3	0	30%
Fuirena	8	5	0	63%
Isolepis	2	1	0	50%
Lipocarpha	4	1	0	25%
Rhynchospora	74	45	4	66%
Schoenoplectus	15	2	0	13%
Scirpus	14	4	0	29%
Scleria	18	4	0	22%
TOTALS	472	122	5	27%

areas of the Southeast…likely will be fruitful" (1998: 18).

Coastal Plain Sedge Phytogeography

Members of the Cyperaceae share many of the same distributional patterns as other vascular plants. Sorrie and Weakley (2001) discuss 27 phytogeographic patterns shown by endemic and near-endemic taxa of the Coastal Plain. Here I recognize 14 patterns of distribution shown by sedges. More detailed descriptions for most of these phytogeographic patterns may be found in Sorrie and Weakley (2001).

1. Southern New England to Delmarva Peninsula (Fig. 2). Specialized habitats such as maritime heathlands, sandplain grasslands, coastal plain ponds, salt ponds, and Delmarva bays support at least 15 endemic vascular plant taxa in this region. Colonization following glacial maxima probably occurred via long-distance dispersal events or from populations that occupied nearby refugia on the now-submerged continental shelf (Sorrie, 1998; Edwards & Sharitz, 2000). Two sedge species show this pattern.

Rhynchospora knieskernii J. Carey (endemic to southern New Jersey), *Scirpus longii* Fernald (recent discoveries inland suggest that *S. longii* should no longer be considered a strict Coastal Plain endemic; nonetheless, it almost certainly evolved there).

2. Atlantic maritime (Fig. 3). Two sedge species occur from southern Maine to Georgia in saline to brackish marshes, interdune wet swales, and salt ponds. *Carex calcifugens* Naczi has been collected in maritime forests and coastal and near-coastal shell mounds, but too many populations occur inland to warrant this species' inclusion here. Two taxa: *Bolboschoenus novae-angliae* (Britton & A. Br.) S. G. Sm., *Cyperus filicinus* Vahl.

3. Southeastern North Carolina to northeastern South Carolina (Fig. 2). Recognition of the Cape Fear Arch region of the Carolinas as a center of plant speciation was documented by LeBlond (2001). Two taxa: *Carex lutea* LeBlond and an undescribed taxon affined to *Scleria.*

4. Essentially Floridian, ranging to southern South Carolina and southern Alabama (Fig. 2). Some of these taxa occupy only a small portion of this range; a few extend farther west on the Gulf Coastal Plain. This is

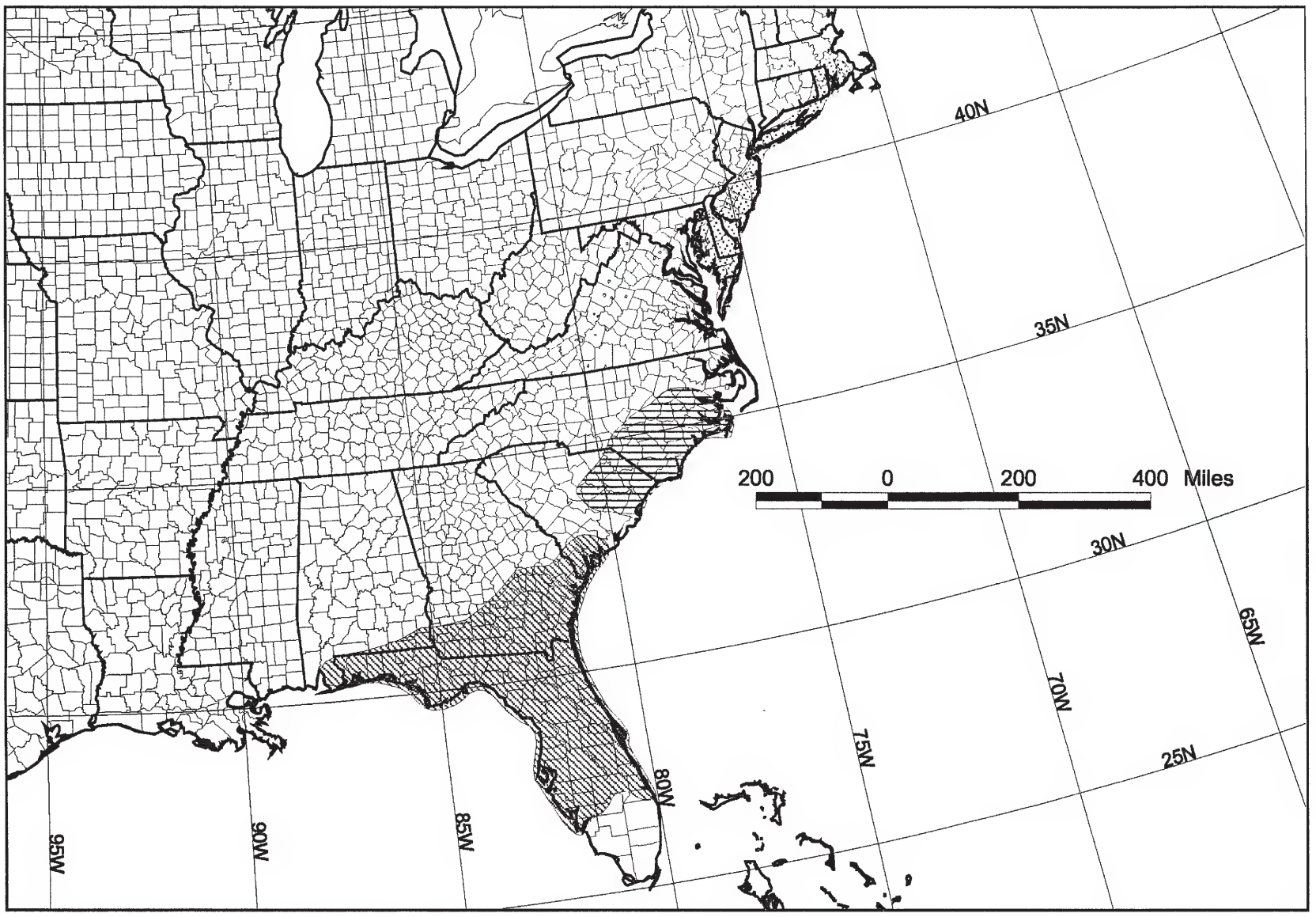

Figure 2. Pattern 1: southern New England to Delmarva Peninsula (dots). Pattern 3: southeastern North Carolina to northeastern South Carolina (horizontal lines). Pattern 4: essentially Floridian, ranging to southern South Carolina and southern Alabama (wavy slanted lines).

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one of the two most important areas of vascular plant endemism within the Coastal Plain. Fifteen taxa: *Bulbostylis warei* (Torr.) C. B. Clarke, *Carex dasycarpa* Muhl., *C. fissa* Mack. var. *aristata* F. J. Herm., *C. paeninsulae* Naczi, E. L. Bridges & Orzell, *C. vexans* F. J. Herm., *Cyperus distinctus* Steud. (disjunct to northwestern Bahamas), *C. ovatus* Baldwin, *Eleocharis microcarpa* Torr. var. *microcarpa* (disjunct to western Cuba), *Rhynchospora fernaldii* Gale, *R. harveyi* W. Boott var. *culixa* (Gale) Kral, *R. megaplumosa*, *R. pineticola* C. B. Clarke, *R. punctata* Elliott, *R. solitaria* R. M. Harper, *R. sulcata* Gale (synonymized under *R. microcarpa* Baldwin ex A. Gray by Kral in *Flora of North America*).

5. Widespread on the southern Coastal Plain, disjunct to the southern New Jersey–Delmarva Peninsula region (Fig. 4). Rising sea level during the Holocene in Chesapeake Bay has apparently eliminated habitat for these species. Four species: *Rhynchospora careyana* Fernald, *R. harperi* Small, *R. inundata* (Oakes) Fernald (also disjunct to Massachusetts–Rhode Island), *R. oligantha* A. Gray.

6. Longleaf pine range (southeastern Virginia–central Florida–east Texas) (Fig. 5). Longleaf pine (*Pinus palustris* Mill.) and its associated habitats form the core area of endemism on the Coastal Plain, especially at the generic level. Some of the following taxa occupy only a small portion of this range. Patterns 3, 4, 7, and 8 may be considered subsets of the longleaf pattern. Twenty-one taxa: *Bulbostylis ciliatifolia* (Elliott) Fernald var. *ciliatifolia*, *Carex digitalis* Willd. var. *floridana* (L. H. Bailey) Naczi & Bryson, *C. elliottii* Schwein. & Torr., *C. floridana* Schwein., *C. gholsonii* Naczi & Cochrane, *C. godfreyi* Naczi, *C. tenax* Chapm., *Cyperus lecontei* Torr. ex Steud., *C. tetragonus* Elliott s. str., *Eleocharis baldwinii* (Torr.) Chapm., *E. vivipara* Link, *Fimbristylis decipiens* Kral, *Fuirena breviseta* (Coville) Coville, *Rhynchospora baldwinii* A. Gray, *R. ciliaris* (Michx.) C. Mohr, *R. decurrens* Chapm.,

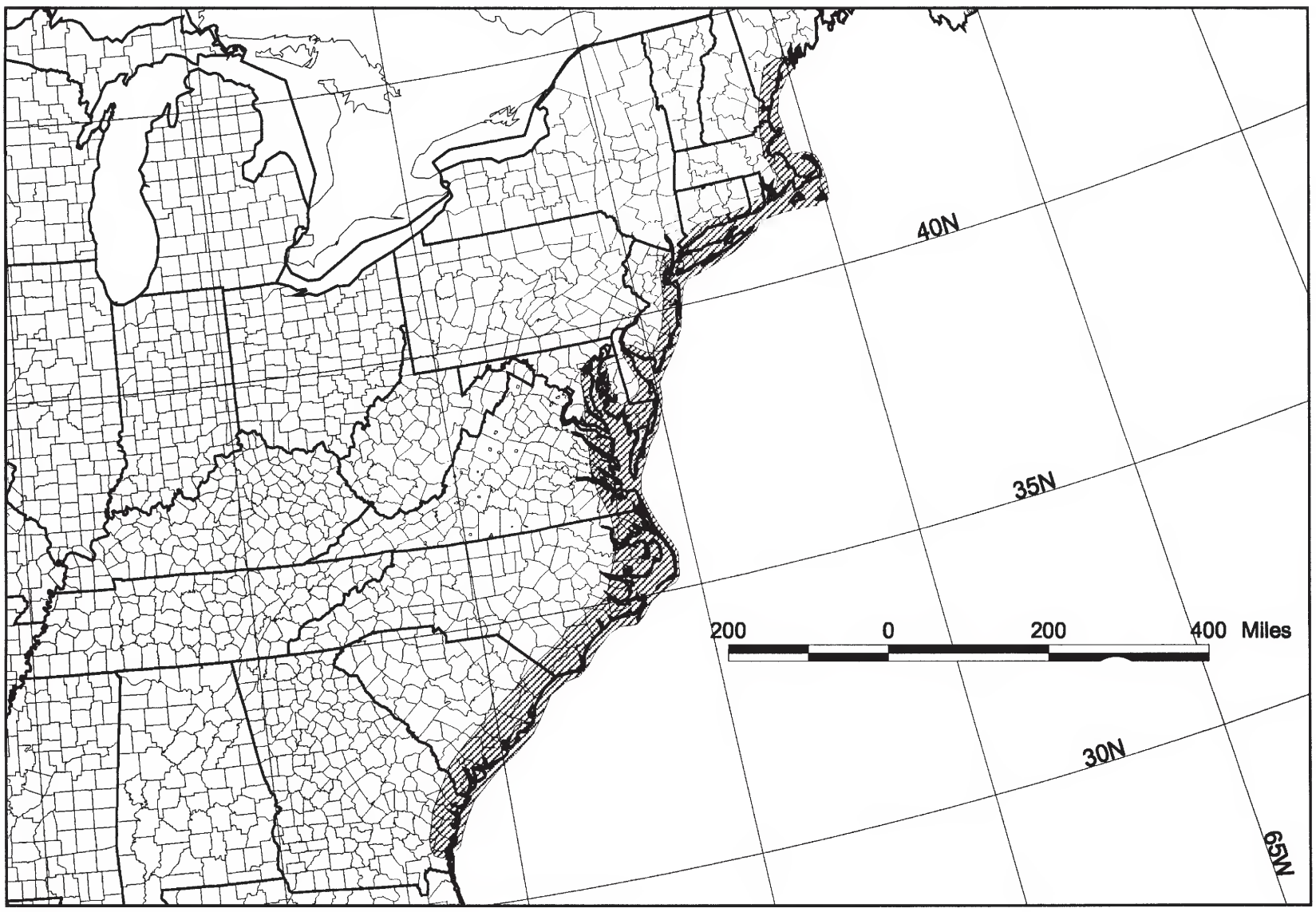

Figure 3. Pattern 2: Atlantic maritime.

R. elliottii A. Dietr., *R. fascicularis* (Michx.) Vahl var. *distans* (Michx.) Chapm. (disjunct to Bermuda), *R. megalocarpa* A. Gray, *Scirpus lineatus* Michx., *Scleria ciliata* Michx. var. *glabra* (Chapm.) Fairey.

7. East Gulf Coastal Plain (southwestern Georgia–northwestern Florida–southeastern Alabama) (Fig. 6). Although a very important area of endemism for vascular plants (122 endemic taxa; Sorrie & Weakley, 2001), surprisingly few Cyperaceae are strictly confined to the EGCP. Those in Pattern 8 no doubt originated within the EGCP, but have managed to populate the Carolinas via dispersal events. Three species: *Carex baltzellii* Chapm. ex Dewey, *C. thornei* Naczi, *Rhynchospora curtissii* Britton.

8. Primarily East Gulf Coastal Plain, disjunct to the Carolinas (Fig. 6). The reasons for this disjunction are as yet unclear, but the intervening area of southeastern Georgia and southern South Carolina supports mostly pine flatwoods, whereas the following species (except *Rhynchospora crinipes* Gale) require seepage bog communities. Habitat destruction and incomplete inventory in the hiatus area also have contributed to a lack of records. Seven taxa: *Carex turgescens* Torr., *Rhynchospora cephalantha* A. Gray var. *attenuata* Gale, *R. compressa* J. Carey ex Chapm., *R. crinipes*, *R. leptocarpa*, *R. macra* (C. B. Clarke) Small, *R. stenophylla* Chapm.

9. West Gulf Coastal Plain (western Louisiana–southeastern Texas–southeastern Oklahoma–southern Arkansas) (Fig. 6). This region has been shown to be an important center of endemism for taxa inhabiting xeric communities (MacRoberts et al., 2002), so it is not surprising that only three sedges, all wetland inhabitants, are endemic: *Cyperus cephalanthus* Torr. & Hook., *Fuirena bushii* Kral, *Rhynchospora glomerata* (L.) Vahl var. *angusta* Gale.

10. Widespread on the Coastal Plain, disjunct to the Great Lakes region (Fig. 7). Six species. Note: there are a number of other Cyperaceae that are disjunct to the Great Lakes (Reznicek, 1994). Although they may have originated on the Coastal Plain, they now occupy ranges that are now too broad to be considered endemic or near-endemic to it: *Eleocharis melanocarpa* Torr., *E. tricostata* Torr., *Fuirena*

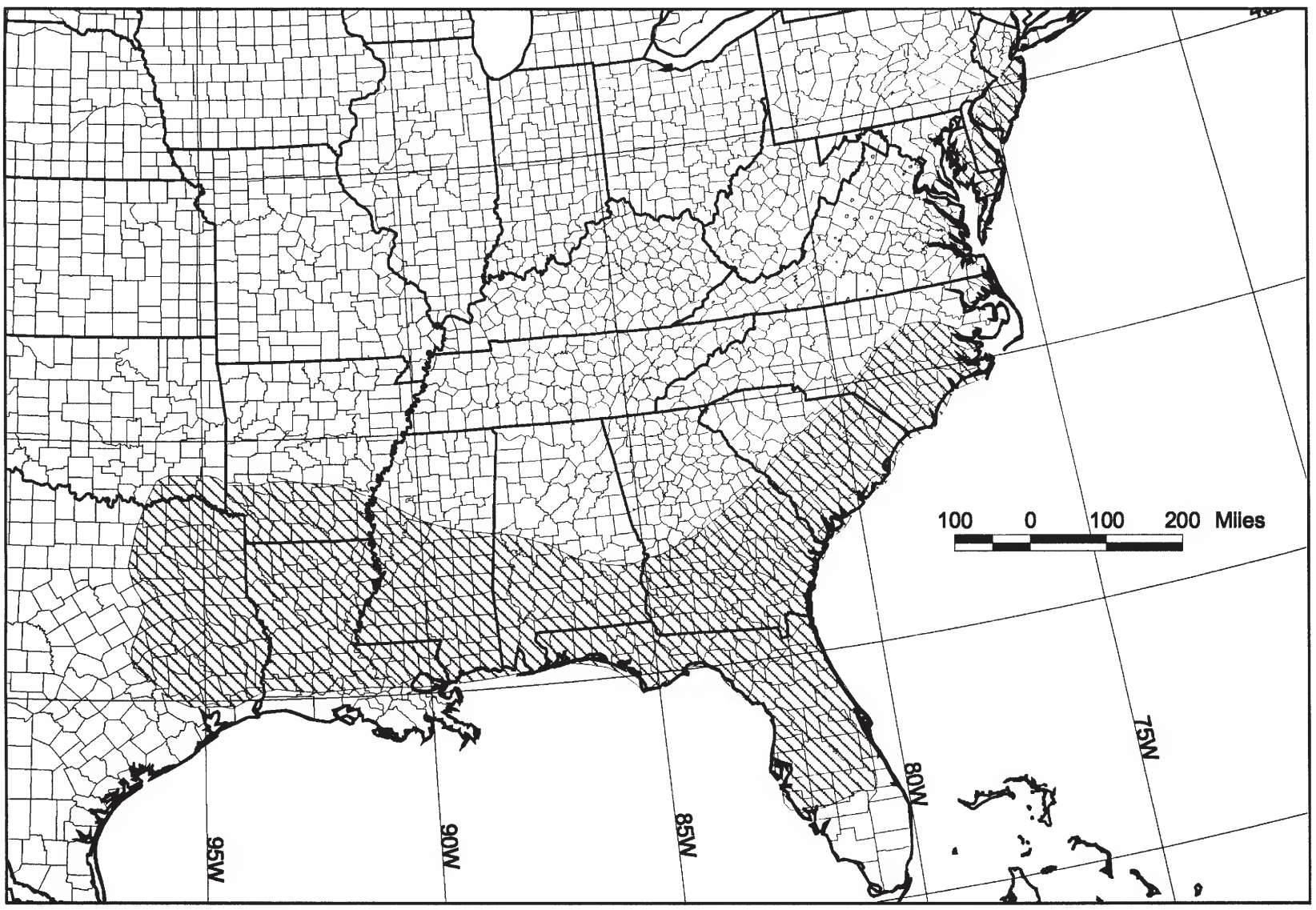

Figure 4. Pattern 5: widespread southern taxa, disjunct to the southern New Jersey–Delmarva Peninsula region.

pumila (Torr.) Spreng., *Lipocarpha maculata* (Michx.) Torr., *Rhynchospora scirpoides* (Torr.) A. Gray, *Scleria reticularis* Michx. s. str.

11. Widespread on the Coastal Plain, disjunct to central Tennessee, northwestern Georgia, and northeastern Alabama (Fig. 7). Sorrie and Weakley (2001) restrict this disjunction to Tennessee and Kentucky. Additional research suggests that taxa disjunct to northern Alabama and Georgia may be part of the same historical migration events. Fourteen taxa: *Carex glaucescens* Elliott, *C. lonchocarpa* Willd., *C. verrucosa* Muhl., *Eleocharis tuberculosa* (Michx.) Roem. & Schult., *Rhynchospora chalarocephala* Fernald & Gale, *R. debilis* Gale, *R. globularis* (Chapm.) Small var. *globularis*, *R. gracilenta* A. Gray, *R. inexpansa* (Michx.) Vahl, *R. latifolia* (Baldwin ex Elliott) W. W. Thomas, *R. microcephala* (Britton) Britton, *R. perplexa* Britton, *R. thornei* Kral, *R. torreyana* A. Gray.

12. Widespread on the Coastal Plain, disjunct to western Cuba, northwestern Bahamas, Belize, or elsewhere in the Caribbean Basin (Fig. 8). Some of these taxa may eventually prove to be too common to be considered rare or uncommon disjuncts, but I include them until better data are at hand. Although not proven, Caribbean islands may have provided important avenues of interchange between the North American Coastal Plain and the rich Neotropical Cyperaceae (particularly *Rhynchospora*, *Cyperus*, and *Scleria*) of Central America and South America. Thomas (1994) was a critical source in determining disjunctions to Central America. Seventeen taxa: *Bulbostylis stenophylla* (Elliott) C. B. Clarke (Cuba), *Cyperus distinctus* (Bahamas), *Eleocharis microcarpa* var. *microcarpa* (Cuba), *Fuirena scirpoidea* Michx. (Cuba, Nicaragua), *Rhynchospora chapmanii* M. A. Curtis (Belize, Nicaragua), *R. globularis* var. *pinetorum* (Britton & Small) Gale (Cuba, Jamaica, Puerto Rico), *R. grayi* Kunth (Cuba), *R. harperi* (Belize), *R. macra* (Nicaragua), *R. microcephala* (Cuba), *R. mixta* Britton (Cuba, Haiti, Jamaica), *R. perplexa* (Cuba, Dominican Republic, Jamaica), *R. pineticola* (Cuba), *R. pleiantha* (Kük.) Gale (Cuba), *R. wrightiana* Boeckeler (Cuba), *Scleria baldwinii* (Torr.) Steud. (Bahamas, Cuba), *S. curtissii* Britton (Cuba).

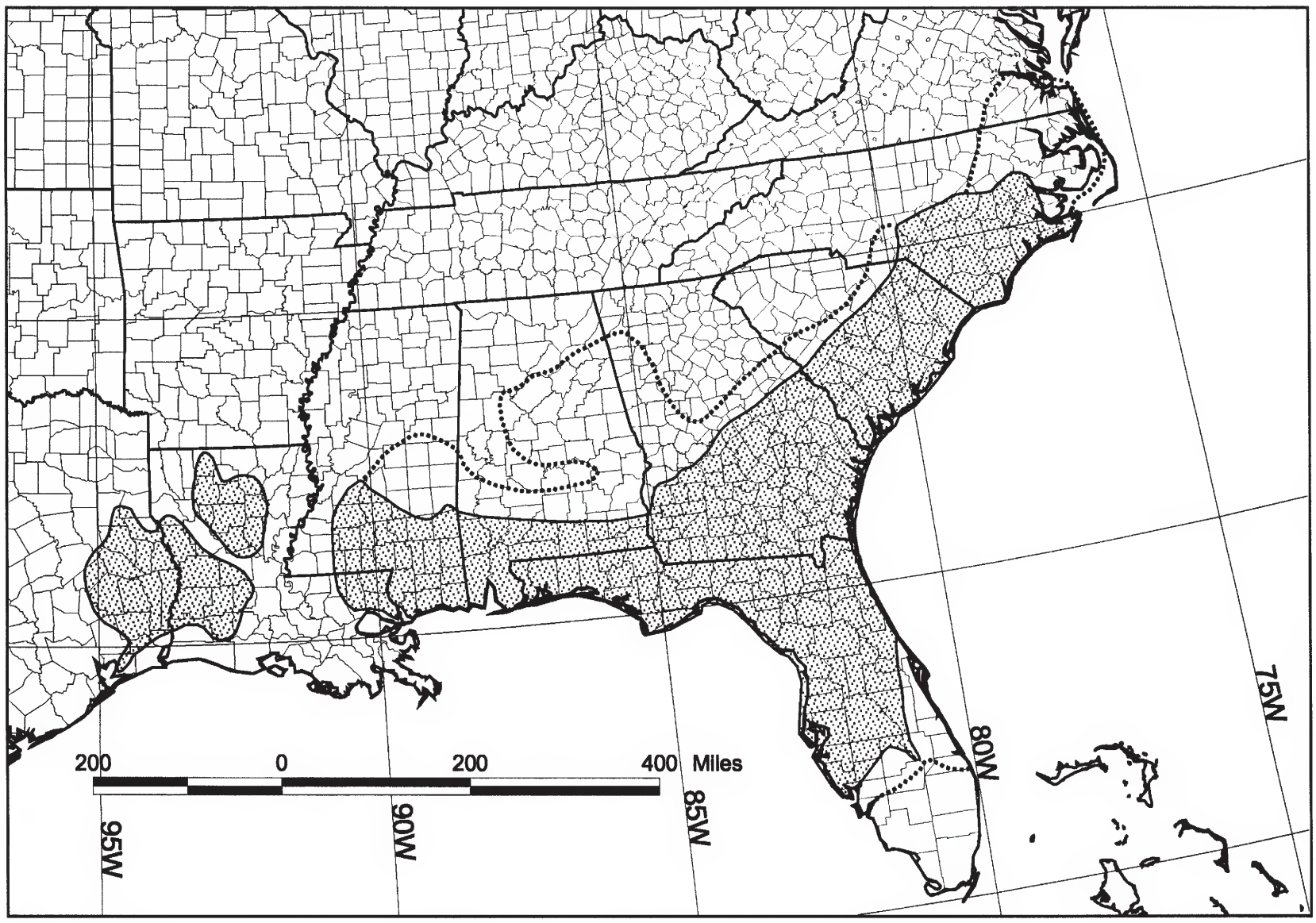

Figure 5. Pattern 6: longleaf pine range (southeastern Virginia–central Florida–east Texas). Area of fine dots represents area where longleaf was formerly continuous; coarse dotted line represents inland limit and area with scattered occurrences.

13. Widespread on the Coastal Plain, including the Mississippi Embayment (Fig. 8). The Embayment itself is a very minor center of plant endemism (five species, no sedges), but has been a conduit for exchange between northern and southern floras. Four taxa: *Carex gigantea* Rudge, *C. socialis* Mohlenbr. & Schwegman (not quite endemic to the Coastal Plain, but probably evolved there), *Eleocharis tortilis* (Link) Schult., *Scirpus divaricatus* Elliott.

14. Amphitropical. New World species with two widely disjunct centers of distribution are known in many families of plants. Perhaps the most famous examples are the numerous taxa that inhabit California and Chile (Raven, 1963). Allred (1981), Solbrig (1972), and Wood (1972) discuss other disjunctions. The following six taxa appear to fit the amphitropical pattern, subject to additional collecting and taxonomic work: *Bolboschoenus robustus* (Pursh) Soják, *Carex aureolensis* Steud., *Cyperus cephalanthus*, *C. reflexus* Vahl (including *C. fraternus* Kunth), *Eleocharis cylindrica* (including *E. texana* Britton), *E. macrostachya* Britton.

Cyperus ochraceus Vahl and *C. virens* Michx. are less strikingly disjunct, ranging from the southeastern United States to extreme northern South America, then disjunct to southern South America.

Conclusion

The Coastal Plain FP harbors a major segment of the North American Cyperaceae. The diversity and endemism of the Coastal Plain sedges are greater than that for any other floristic province in the continent. With increased loss of natural habitats, conversion of uplands to tree plantations, drainage of wetlands, and general fragmentation of the landscape by human population growth, many Cyperaceae are considered endangered or threatened over large portions of their ranges (NatureServe, 2003). In addition, some sedges have naturally

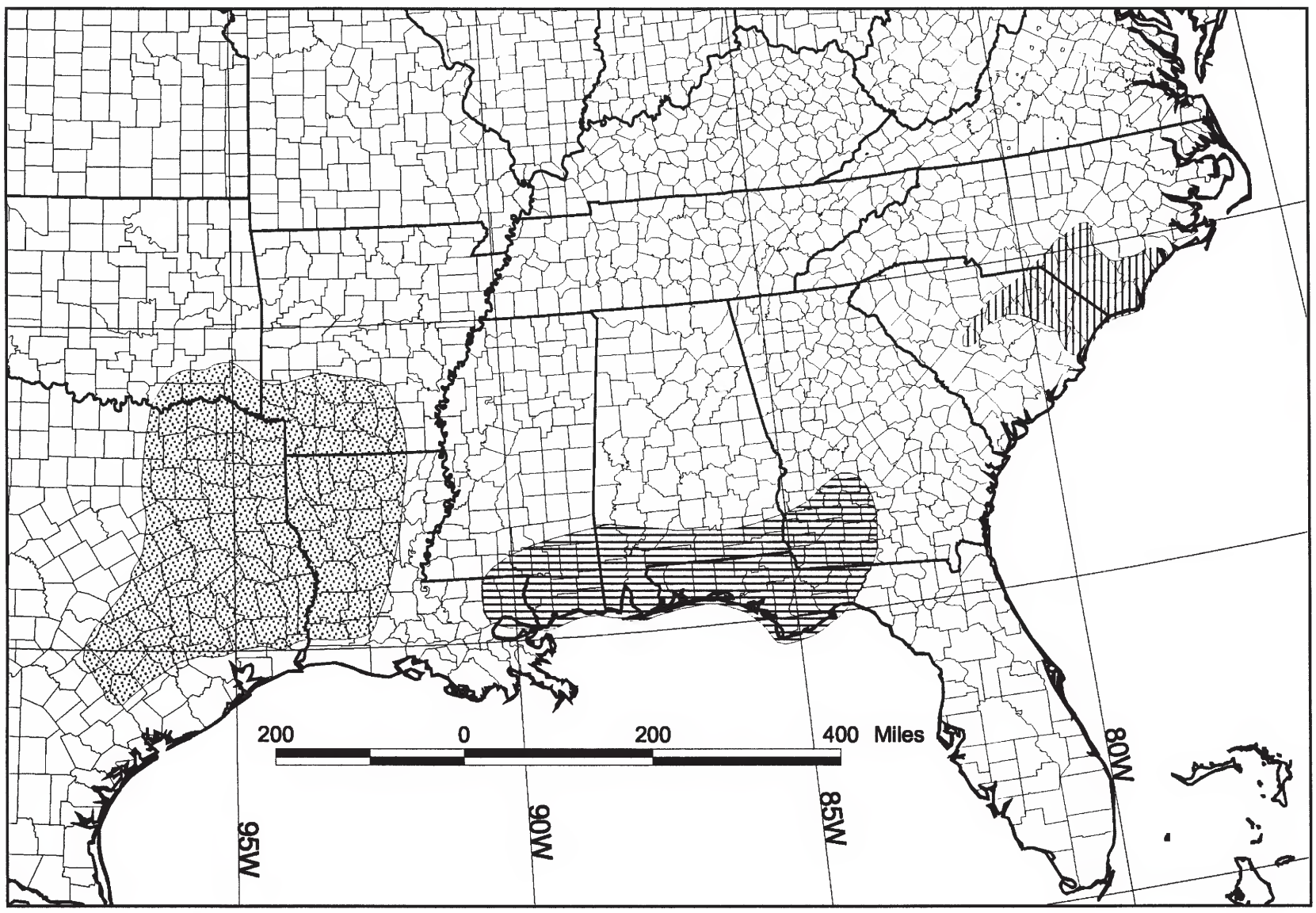

Figure 6. Pattern 7: East Gulf Coastal Plain (southwestern Georgia–northwestern Florida–southeastern Alabama) (horizontal lines). Pattern 8: primarily East Gulf Coastal Plain, disjunct to the Carolinas (vertical lines). Pattern 9: West Gulf Coastal Plain (western Louisiana–southeastern Texas–southeastern Oklahoma–southern Arkansas) (dots).

highly restricted ranges. Examples include *Carex lutea*, two counties in North Carolina; *Fimbristylis perpusilla* R. M. Harper, scattered in 11 counties in seven states; and *Rhynchospora solitaria*, vouchered from two counties in Georgia and reported from two others. Protection of important sites must be done soon if we are to maintain this remarkable diversity of sedges.

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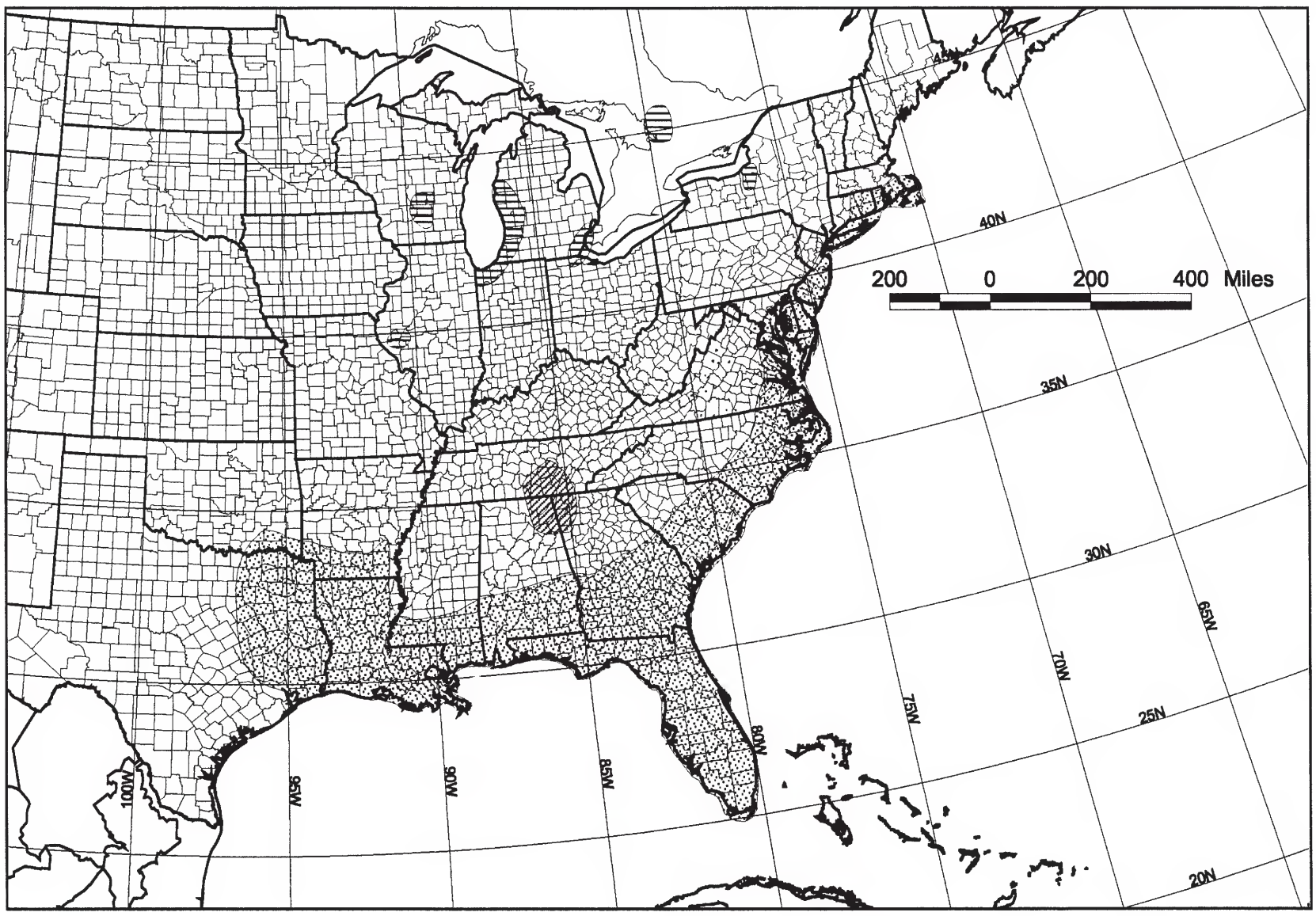

Figure 7. Pattern 10: widespread (dots), disjunct to Great Lakes region (horizontal lines). Pattern 11: widespread, disjunct to central Tennessee, northwestern Georgia, and northeastern Alabama (slanted wavy lines).

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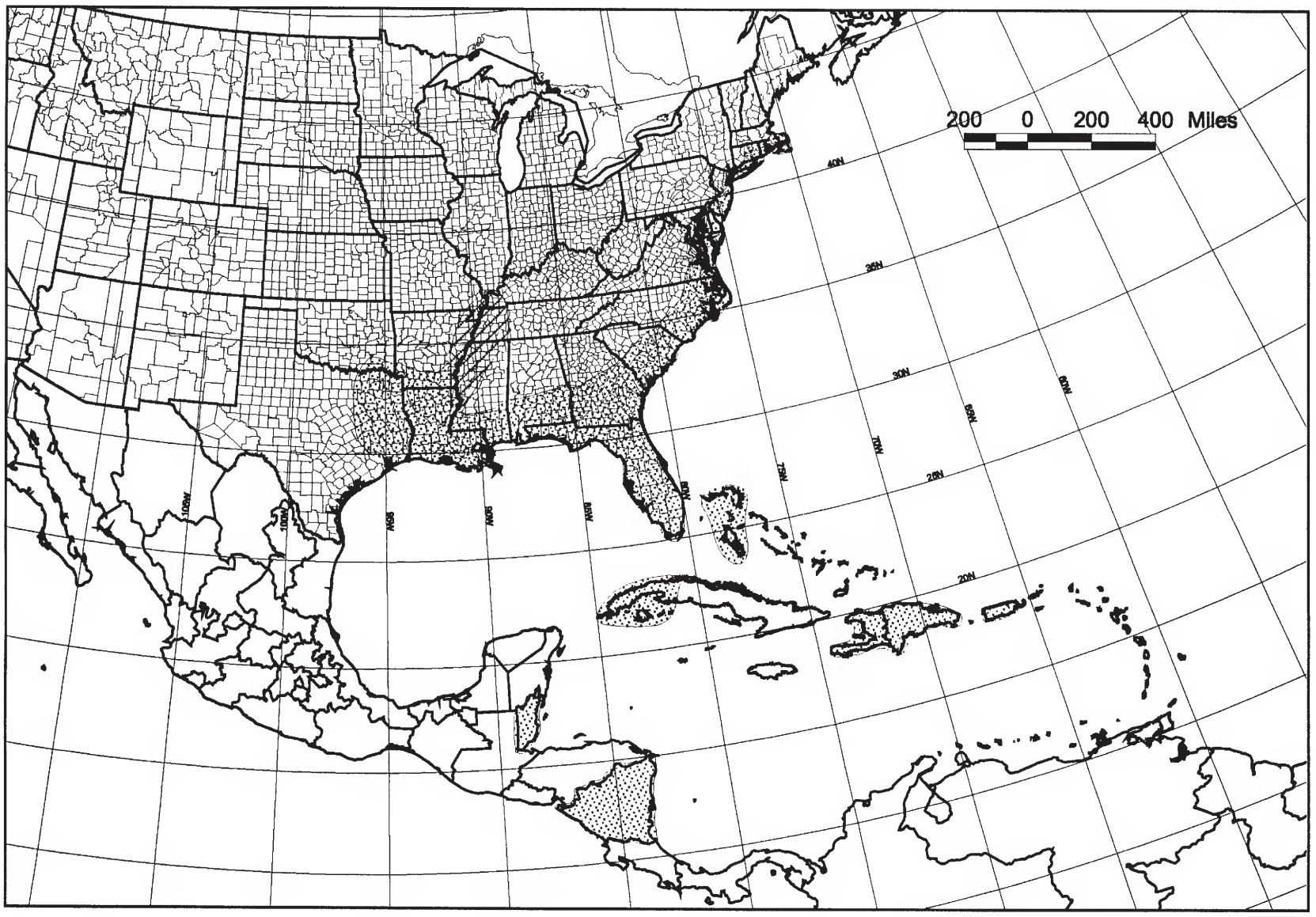

Figure 8. Pattern 12: widespread (dots), disjunct to western Cuba, northwestern Bahamas, Belize, or elsewhere in the Caribbean Basin (dots). Pattern 13: widespread, including the Mississippi Embayment (slanted lines).

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Chapter 4

Carex (Cyperaceae) of the Kisatchie National Forest, Louisiana, U.S.A.

Philip E. Hyatt

ABSTRACT Plant surveys on the Kisatchie National Forest (Forest) in northern Louisiana, U.S.A., and review of herbarium *Carex* L. (Cyperaceae) specimens resulted in a list of 59 *Carex* taxa. One globally rare, U.S. Forest Service regionally listed sensitive species, *C. decomposita* Muhl., occurs at a single location on the Forest (ranked G3 and S1). One state-rare species, *C. meadii* Dewey, occurs in several small remnant prairies (ranked G4G5 and S2) on the Forest. A third rare-to-Louisiana species, *C. stricta* Lam., is known from Louisiana and on the Forest from a historical collection of a single culm in 1936. The distribution of *Carex* taxa is compared to the ecological classification of landscape-scale plant communities.

KEY WORDS *Carex*, Cyperaceae, Kisatchie National Forest, Louisiana.

A review of herbarium collections combined with eight years of fieldwork has yielded a list of 59 *Carex* L. taxa for the Kisatchie National Forest (Forest), Louisiana, U.S.A. The Southern Forest Range Program (SFRP) herbarium contains *Carex* specimens from as far back as the 1930s. Several researchers added specimens during the 1950s, although the herbarium suffered from a fire on November 18, 1959 (Alexandria Town Talk, 1959a, b). This newspaper reported the building as "a total loss" (Alexandria Town Talk, 1959a, b: 1). Nevertheless, many smoke-damaged specimens were retrieved from the herbarium. Harold Grelen collected SFRP specimens from the Forest from April 4, 1962 (collection number 20) to April 28, 1983 (collection number 2006). Grelen worked as a range researcher and collected *Carex* primarily when it was found in range research plots. Records from SFRP, six other herbaria, and recent fieldwork form the basis for this paper.

Materials and Methods

The present study, specifically of *Carex*, on the Forest began in February 1995. This work included cursory surveys of a wide variety of habitats across the Forest, including all districts. Figure 1 presents outlines of northern Louisiana counties with administrative boundaries for the Forest. Collection sites for all *Carex* taxa from the Forest are shown in Figure 2. The Forest encompasses 603,769 acres (Kisatchie National Forest, 1999). Surveys were conducted primarily on the Catahoula and Winn Districts, but occasionally included all other land units of the Forest. Infrequently, fieldwork centered specifically on adding species to those districts where fewer *Carex* species had been found. Six herbaria, LAF, LSU, LTU, NATC, NLU, and SFRP were checked for records (Holmgren & Holmgren, 1998 onward). Data were compiled using the Forest's ArcView geographic information system, which allowed the electronic mapping of locations. For older collections accuracy is usually down to one square mile, based on label information. Some locations were accurate to the quarter quarter section. Collections made during 2002 were accurately located within about 50 feet using a Garmin III or V global positioning system. Duplicates of new collections were distributed widely, but primarily to SFRP, MICH, LSU, and NLU, in that order. Nomenclature follows *Flora of North America* (Flora of North America Editorial Committee, 2002).

Results

The landtype associations are described in the Final Environmental Impact Statement for the Revised Land and Resource Management Plan for the Forest (Kisatchie National Forest, 1999). This management plan provides detailed information on the habitats of the Forest (pp. 3-115–3-162). The Forest is divided into nine landtype associations (LTAs). See Figure 1 for names and locations of each LTA. These LTAs can be grouped into four broad landscape-scale communities: (a) longleaf pine (LTAs 1, 2, 5, 6); (b) shortleaf pine/oak–hickory (LTAs 3, 8, 9); (c) mixed hardwood–loblolly pine (LTA 4); and (d) riparian and floodplain areas (LTA 7). Habitats for *Carex* vary widely by species, to the point that essentially every acre of the Forest potentially supports at least one species.

MacRoberts (1988) reports 75 *Carex* taxa for Louisiana; Thomas and Allen (1993a) report 70 taxa for the state; both do so without citing varieties in most cases. Several varieties are recognized in this work. Fifty-nine *Carex* taxa were detected from the Forest. Of these, 34 taxa occur on three or more of the Forest's six primary geographic/administrative units as listed below. The number of taxa per unit are: Caney, 29; Catahoula, 40; Evangeline, 42; Kisatchie, 30; Winn, 43; and Vernon, 23. The unit (Vernon Unit of the Calcasieu District) with smaller total numbers of taxa recorded is also the least-studied unit. Each district (or unit) apparently supports about the same number of taxa. The numbers of taxa and the distribution of mapped collections center on areas surveyed and only rarely reflect occurrence district-wide; for example, the Caney and Middle Fork units of the Caney District each have five known taxa, while the well-searched Corney Unit of the same district has 22. Twenty-two *Carex* taxa occur infrequently or in specialized habitats, so that they are less commonly encountered. Most (but not all) of these taxa would be expected on the other units. One globally rare G3 U.S. Forest Service regionally listed sensitive species, *C. decomposita* Muhl., occurs at a single location on the Forest. One state-rare S2 species, *C. meadii* Dewey, occurs in

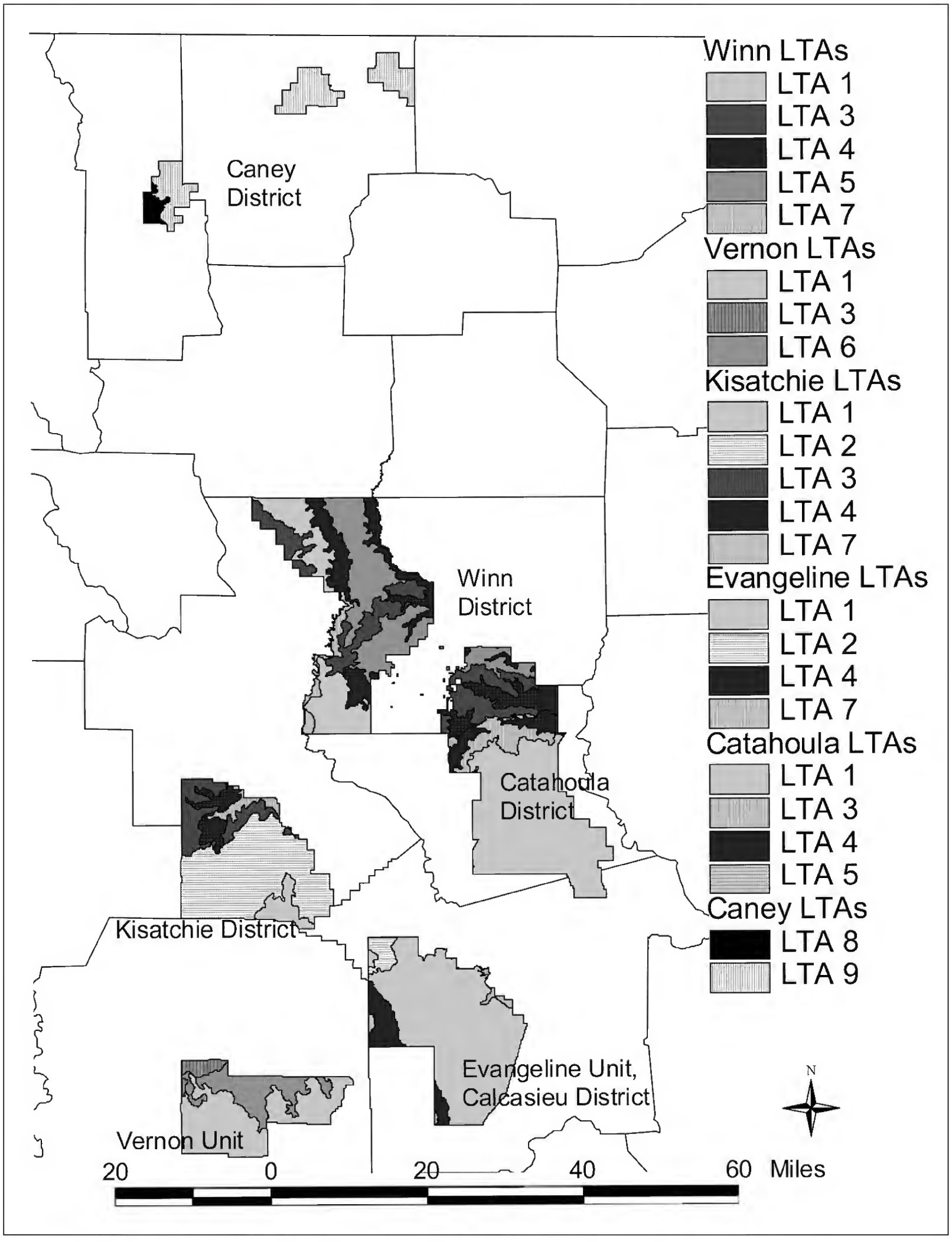

Figure 1. Land type associations (LTAs) of the Kisatchie National Forest on a background of parish boundaries: LTAs 1, 2, 5, and 6 are longleaf pine communities (named high terrace rolling uplands, Kisatchie sandstone hills, Winn rolling uplands, Fort Polk rolling uplands, respectively); LTAs 3, 8, and 9 are shortleaf pine/oak–hickory communities (named undulating clayey uplands, Caney Lakes loamy uplands, and north Louisiana clayey uplands, respectively); LTA 4 is a mixed hardwood–loblolly pine community (named alluvial floodplains and stream terraces); LTA 7 is frequently flooded bottomland plant community (named the Red River alluvial plain).

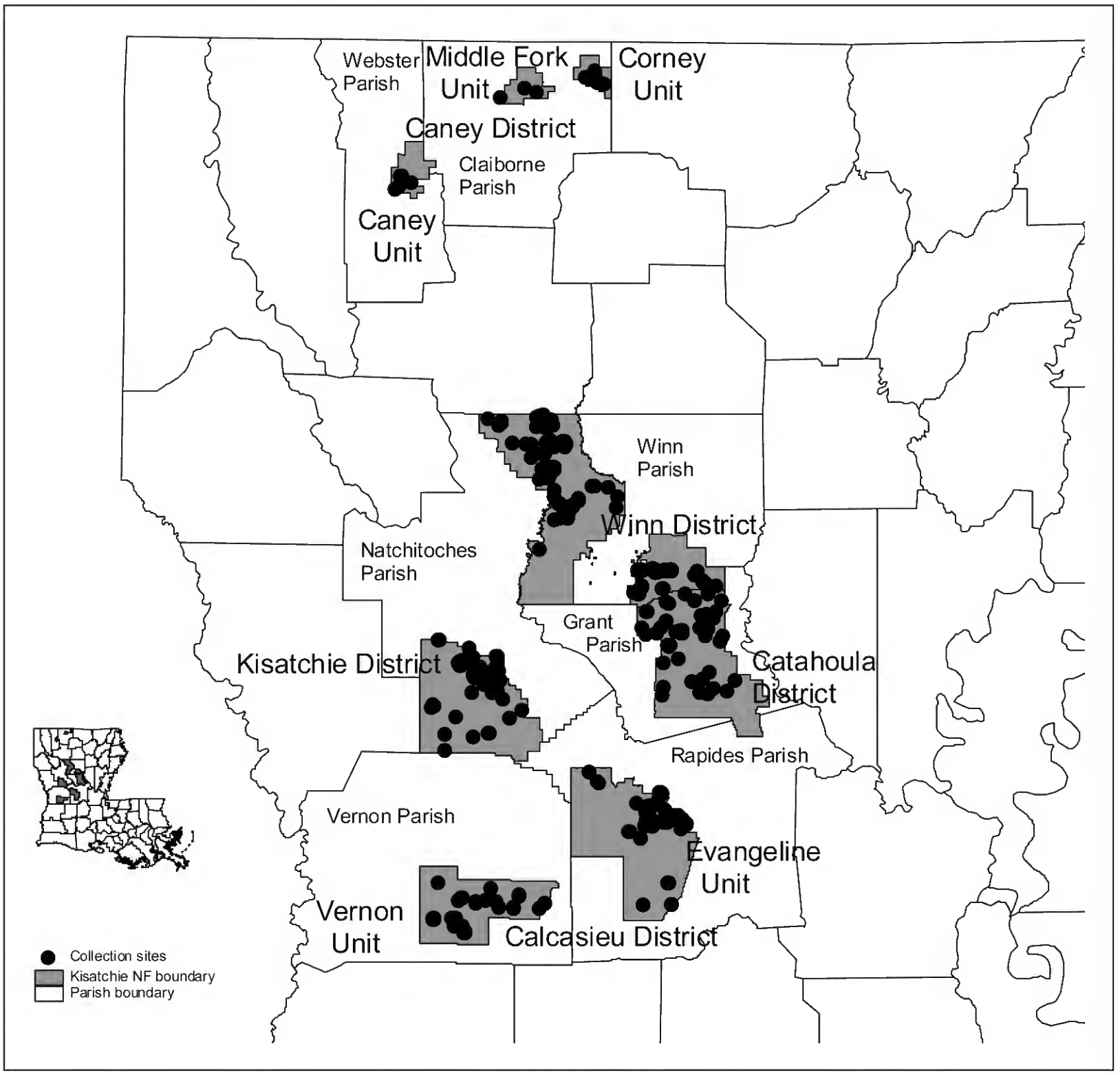

Figure 2. Vicinity map for the Kisatchie National Forest and for *Carex* collection sites.

several small remnant prairies. A third rare-to-Louisiana species, *C. stricta* Lam., is known from Louisiana and on the Forest from a historical collection of a single culm in 1936; it should be ranked SH as a historic species in Louisiana.

For the following taxa, limited synonymy, habitat, frequency, comment, collection number, and herbaria are provided followed by comments. Lastly, S ranks are provided when available from NatureServe (2006). Most *Carex* taxa are listed for Louisiana as SNR (not yet ranked) by NatureServe (2006). Collection numbers are those of the author unless otherwise noted and only one voucher per taxon is cited. Habitats and frequencies listed represent only those given by collectors or noted for the Forest. Frequencies range from abundant to common, frequent, occasional, rare (one to three sites on the Forest), or historic (no collections in the past 20 years). Figures 3 to 7 provide maps of collection sites for each taxon listed, and a summary map with collection sites for all taxa.

LIST OF *CAREX* TAXA FOR THE KISATCHIE NATIONAL FOREST

Carex abscondita Mack.

Streamside zones of larger streams, usually on sandy soils; locally abundant, widespread in its habitat; not reported for Louisiana by Thomas

Figure 3. *Carex abscondita* to *C. cephalophora* collection sites.

and Allen (1993a); *8003* MICH, SFRP. Rosen (2001) confirmed this taxon for the state in eight Louisiana parishes based primarily on Hyatt's collections. This species occupies a narrow strip of habitat along natural levees and adjoining low slopes. This causes many generalist collectors to overlook it despite its often local abundance.

Carex albicans Willd. ex Spreng. var. *australis* (L. H. Bailey) Rettig

[= *Carex physorhyncha* Liebm.] Mesic woodlands, wooded slopes, near streams; locally common; *8004* MICH, SFRP. This taxon blooms early and occupies small microsites such as wet springheads and seeps, and is thus not found by many collectors. Careful and early season search will reveal it at many locations, often in low numbers. S3S4.

Carex albolutescens Schwein.

Wetland backwater swamps away from flowing streams; occasional; *8011* MICH, SFRP. This taxon is much less ruderal than *Carex longii* Mack. and often requires searches in more natural habitats to locate it successfully.

Carex atlantica L. H. Bailey subsp. *capillacea* (L. H. Bailey) Reznicek

[= *Carex howei* Mack.] Seeps, swamps, often epiphytic on cypress knees, tree bases; locally abundant; *6220* MICH, SFRP. This sedge's culms have the curious habit of continuing to grow after they initially mature. These culms extend to greater than 1 m long and, while they die in winter, they will often remain with the plant into the next blooming season.

Carex aureolensis Steud.

[= southern version of *Carex frankii* Kunth s.l.] Ruderal wetlands, woodland road ruts, swamps; occasional; *10,251* MICH, SFRP. Formerly considered *C. frankii* s.l. in Louisiana and elsewhere. This taxon has rhizomes usually > 10–30 cm long while *C. frankii* s. str. is caespitose. The pistillate scales also have a ± 2 mm (wider in AZ and NM collections) translucent edge at the base which *C. frankii* lacks.

Carex austrina Mack.

Deep sands, roadsides; rare, known on the Forest only from Saline Bayou roadside, about 2 miles east of Goldonna in Winn Parish and a few other locations in Louisiana; not reported for Louisiana by Thomas and Allen (1993a); *Hyatt & Moore 7389* SFRP.

Carex basiantha Steud.

Riparian floodplains, lower wooded slopes; occasional, locally abundant; reported for Lousiana as *Carex willdenowii* Schkuhr ex Willd. by Thomas and Allen (1993a); *6178* MICH, SFRP. Habitat and collection frequency is similar to *C. abscondita*. *Carex basiantha* usually occurs on slightly drier sites that are less subject to stream scour than *C. abscondita.* It especially prefers low slopes along larger streams rather than natural levees but may occur in both types of habitat.

Carex blanda Dewey

Low woods, riparian areas; occasional; *8442* MICH, SFRP. This taxon is less ubiquitous in Louisiana than farther north.

Carex bromoides Schkuhr ex Willd. subsp. *bromoides*

Swamps, floodplains; occasional, locally abundant; *6524* MICH, SFRP. Another easily overlooked taxon for the casual collector; locating this taxon requires a willingness to enter its habitat and brave the presence of water moccasins. *Carex bromoides* is readily located in swamp edges, especially around the swollen bases of wetland trees.

Carex bulbostylis Mack.

Riverine wetlands; locally abundant; not reported for Louisiana by Thomas and Allen (1993a); *8108* MICH, SFRP. *Carex bulbostylis* forms extensive dense colonies in the floodplains of the largest streams, such as along the Red River with its broad floodplain.

Carex caroliniana Schwein.

Ruderal roadsides, sunny wetlands; occasional; *7035* SFRP.

Carex cephalophora Muhl. ex Willd.

Mesic woods; infrequent; *8007* SFRP. Like *Carex blanda*, this taxon is much more common to the north of Louisiana.

Carex cherokeensis Schwein.

Woodlands, floodplains; common; *6179* MICH, SFRP.

Carex complanata Torr. & Hook.

Upland woods, ruderal areas; abundant; *7406* SFRP.

Carex corrugata Fernald

Riverine floodplains with *Carex hyalina* Boott

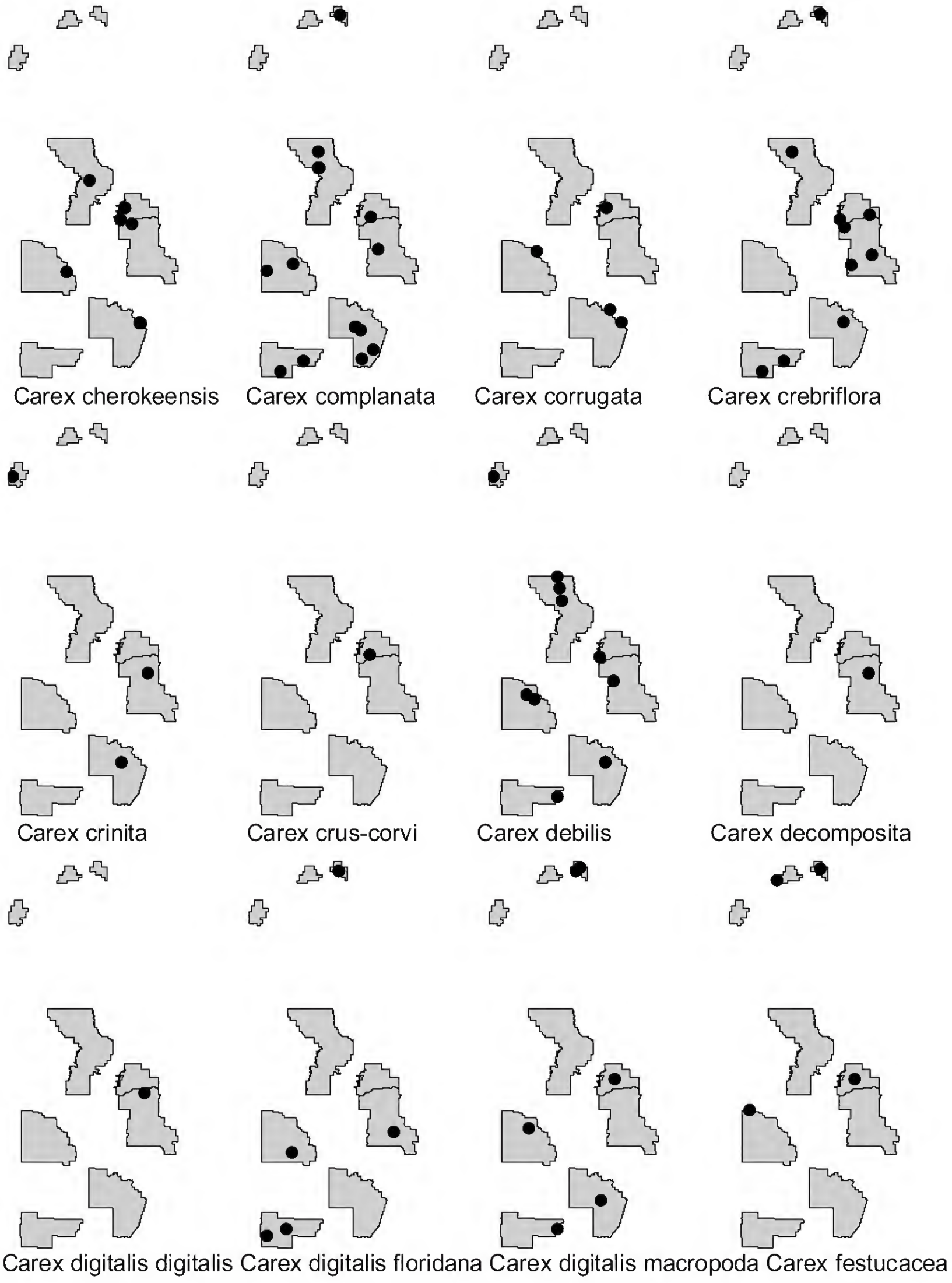

Figure 4. *Carex cherokeensis* to *C. festucacea* collection sites.

and *C. bulbostylis*; locally common; *7058* MICH, SFRP.

Carex crebriflora Wiegand

Floodplains of smaller drainages; locally common; *6867* MICH, SFRP. In Louisiana, this taxon is readily located in its specialized habitat but often overlooked by the casual collector. It seldom occurs on roadsides or along larger drainages. Instead, it thrives along the upper reaches of some of the smallest intermittent streams downstream into small floodplain areas.

Carex crinita Lam. in J. Lamarck et al.

Wetlands, swamps, seeps; occasional; *9581* SFRP.

Carex crus-corvi Shuttlew. ex Kunze

Wetlands, ruderal wetlands; common; *Grelen 856* SFRP.

Carex debilis Michx. var. *debilis*

Streamside, seeps, wetlands, ruderal moist habitats; abundant; *6190* MICH, SFRP.

Carex decomposita Muhl.

Beaver pond; fewer than 50 plants at one site; *6190* LSU, MICH, NLU, SFRP, UARK. Careful searches in numerous wetlands on the Forest have failed to reveal additional sites. NatureServe (2006) lists the species as S2 in Louisiana.

Carex digitalis Willd. var. *digitalis*

Mesic woodlands; infrequent; *6428* MICH, SFRP.

Carex digitalis var. *floridana* (L. H. Bailey) Naczi & Bryson

Mesic woodlands; occasional; *6208* MICH, SFRP.

Carex digitalis var. *macropoda* Fernald

Mesic woodlands, lower slopes, riparian areas; abundant; *8006* MICH, SFRP.

Carex festucacea Schkuhr ex Willd.

Ruderal wetlands, sunny swamps; infrequent; *8548* SFRP.

Carex flaccosperma Dewey

Wetland edges, streamside zones, mesic uplands; common; *6206* SFRP.

Carex gigantea Rudge

Bayou Beouf Research Natural Area riverine floodplain and shore of Corney Lake; rare, locally common; *6522* MICH, SFRP.

Carex glaucescens Elliott

Streamsides, smaller streams than *Carex joorii* L. H. Bailey, wet woodland road ruts; locally common; *7239* SFRP.

Carex glaucodea Tuck. ex Olney

Disturbed woodlands, woodland roads; occasional; *7386* SFRP. Similarity to the ubiquitous *Carex flaccosperma* tends to make this taxon undercollected. *Carex glaucodea* plants often look like stunted plants of *C. flaccosperma*, resulting in failure of some collectors to recognize and collect it. Both taxa like moist habitats, but *C. glaucodea* is more likely to occur in the middle of woodland roads and in campgrounds, parks, and lawns.

Carex granularis Muhl. ex Willd.

Riverine and large stream riparian areas; infrequent, locally common; *7386* SFRP.

Carex hyalina Boott

Bayou Beouf Research Natural Area (Thomas & Allen, 1993b), Red River floodplain; locally abundant, several sites (Reznicek & Hyatt, 1997); *6956.1* LSU, MICH, UARK. The specialized habitat of this taxon caused it to be overlooked until the above 1993 report. Extensive searches in large stream floodplains during the mid-1990s revealed numerous sites with large populations in Rapides Parish and other sites upstream along the Red River in Louisiana. Once a collector learns the habitat, *Carex hyalina* can often be found within seconds within its habitat. The U.S. Fish and Wildlife Service once tracked *C. hyalina* as a C2 species, but following extensive fieldwork throughout the species range since 1995 the species is now listed as G4, and for Louisiana, S3 (NatureServe, 2006).

Carex hyalinolepis Steud.

Swamps; infrequent, locally abundant; *10,208* MICH, PUR, SFRP.

Carex intumescens Rudge

Streamsides, swamps, ditches; abundant; *7042* MICH, SFRP.

Carex joorii L. H. Bailey

Swamps, wetlands, larger streamsides; common; *7719* SFRP. This taxon and *Carex glaucodea* occur in similar wetland habitats, and both can occur in places where the other is expected. A strong trend exists for *C. glaucodea* to occupy sites along smaller wetland streams and woodland/wetland road ruts of seldom-used

Figure 5. *Carex flaccosperma* to *C. lonchocarpa* collection sites.

roads while *C. joorii* inhabits medium to larger streams and associated ruderal wetlands.

Carex leavenworthii Dewey

Lawn weed, roadsides, ruderal areas; occasional; *10,769* SFRP. *Carex leavenworthii* seldom occurs away from human disturbance in Louisiana.

Carex leptalea Wahlenb.

Seeps, streamside wetlands; common; *7719* MICH. This taxon, with *Carex atlantica* and *C. debilis*, flourishes in early spring and dominates the flora of seepy springheads.

Carex lonchocarpa Willd. ex Spreng.

[= *Carex folliculata* L. var. *australis* L. H. Bailey] Wetland streamsides; occasional, locally frequent; reported by Thomas and Allen (1993a) as *C. folliculata*; *7941* MICH, SFRP.

Carex longii Mack.

Ruderal areas, roadsides, wetlands; common; *6431* MICH, SFRP. This taxon seems to have been previously confused with *Carex albolutescens* in Louisiana. *Carex longii* occurs in ruderal settings most of the time while *C. albolutescens* inhabits more natural sites.

Carex louisianica L. H. Bailey

Swamps, large stream wetlands, riparian areas; locally common; *6523* MICH, SFRP.

Carex lupulina Muhl.

Wetlands, swamps, beaver ponds; common; *7549* SFRP.

Carex lurida Wahlenb.

Sunny wetlands, streamsides; common; *8018* MICH, SFRP.

Carex meadii Dewey

Prairies on calcareous soils; infrequent; *MacRoberts 1903* SFRP. This taxon and the next both occur in prairie habitat, often growing together in this very limited habitat. Observers can separate the two by checking the lower side of the leaves or the perigynia for papillae, which *Carex meadii* has and *C. microdonta* Torr. & Hook. lacks. NatureServe (2006) lists the species as S2 in Louisiana.

Carex microdonta Torr. & Hook.

Prairies on calcareous soils; locally abundant; *Hyatt and Moore 10,005* MICH, SFRP. NatureServe (2006) lists the species as S3 in Louisiana.

Carex muehlenbergii Schkuhr ex Willd. var. *muehlenbergii*

Roadsides, sandy soil woodlands; infrequent; *8109* SFRP. Like several species, this taxon occurs much less frequently in Louisiana than it does to the north.

Carex nigromarginata Schwein.

Upland woodlands, more often mesic sites; occasional; including Louisiana reports of *Carex floridana* Schwein.; *6150* MICH, SFRP.

Carex oxylepis Torr. & Hook. var. *oxylepis*

Mesic woodlands, roadsides; occasional; *7936* SFRP.

Carex planispicata Naczi

Mesic and riverine woodlands; infrequent, locally common; *6435* MICH, SFRP. Recently described by Naczi (1999), *Carex planispicata* occurs much less frequently in Louisiana than to the north.

Carex reniformis (L. H. Bailey) Small

Large stream riparian areas; locally common; *6437* MICH, SFRP.

Carex retroflexa Muhl. ex Willd.

Upland woodlands; infrequent; *6963.1* LSU. *Carex retroflexa* occurs much more abundantly north of our area and becomes somewhat difficult to find in central Louisiana.

Carex socialis Mohlenbr. & Schwegman

Bayou Beouf Research Natural Area, riverine floodplains; rare, locally common; *Allen 17,999* NLU. This associate of *Carex hyalina* is another *Carex* of specialized habitats that has been overlooked in Louisiana in the past. It should be sought throughout the Red River floodplain.

Carex squarrosa L.

Cunningham Brake, riverine floodplains; rare; *Mathies 66* NLU. This taxon occurs much less frequently in central Louisiana than it does farther north.

Carex striatula Michx.

Mesic woodlands along streams; common; *6429* MICH, SFRP.

Carex stricta Lam. in J. Lamarck et al.

Streamside; historic; a specimen with a single culm represents this species in Louisiana. Label data indicate that the plant was "common" along streams on April 10, 1936, in Grant Parish in Comp. 53 at about 200 feet elevation, on a gentle north slope on deep sandy loam soil in Longleaf Pine with "Broom sage." This would place it on the Catahoula District somewhere

Figure 6. *Carex longii* to *C. retroflexa* collection sites.

near Jesse Branch. Frederick J. Hermann identified the specimen on November 25, 1946. The author (1995, unpubl. data) and A. A. Reznicek (1998, unpubl. data) confirmed the identification. The habitat listed appears incorrect for this species unless one takes into account the fact that this taxon occurs in bogs and along perennial streams embedded within the habitat listed on the specimen label. Habitat in the area has been modified by timber harvest, making the rediscovery of this species either difficult due to brushy conditions or impossible due to extirpation. The collector, James M. Black, collected hundreds of specimens on the Kisatchie, so the present author does not doubt the record. *James M. Black 27* SFRP.

Carex styloflexa Buckley

Riparian areas; infrequent; *8540* MICH, SFRP.

Carex tenax Chapm. ex Dewey

Sandy woodlands, typically scattered across the landscape covering wide areas but limited to colonies in deep sandy soils; *6444* SFRP. The Louisiana Department of Wildlife and Fisheries previously tracked *Carex tenax* as an S1 species. Extensive fieldwork in the 1990s revealed numerous colonies, often less than an acre each, on the Kisatchie and Winn Districts and in nearby parishes on private lands. This resulted in an S3 rank (NatureServe, 2006) and discontinued tracking by the Forest.

Carex triangularis Boeckeler

Wetlands, ruderal areas; common; *7986* SFRP.

Carex tribuloides Wahlenb.

Wetlands, beaver ponds, swamps, streamside, ruderal sites; abundant; *10,210* MICH, SFRP.

Carex typhina Michx.

Backwater wetlands of large streams; infrequent, locally common; *7194* LSU, SFRP.

Carex umbellata Schkuhr ex Willd.

Upland hardwoods; infrequent; *Hyatt 7902* MICH, SFRP. Hyatt (1998a) reported this species new to Louisiana and provides statewide distribution. Collectors previously overlooked this early-spring species because of its tendency to become embedded in lawns and because of its short culms that reach only a few centimeters above the ground's surface. Woodland and lawn occurrences should be frequent in northern Louisiana based on limited surveys there and extensive surveys in Arkansas. The taxon appears with significant, but lower, frequency as one proceeds south until it becomes somewhat difficult to find in central Louisiana, especially south of Alexandria.

Carex venusta Dewey

Streamsides; rare; *Allen 14,039* NLU. NatureServe (2006) lists this taxon as S1 for Louisiana. The author searched extensively for it, but found only the ubiquitous *Carex debilis* in the field.

Discussion

Comparison of the Kisatchie *Carex* flora to other areas shows that the number of species declines from north to south in North America north of Mexico. For example, the present study documents 59 taxa on the Forest. Thomas and Allen (1993a) reported 70 taxa for all of Louisiana, while not recognizing some subspecific taxa recognized here. Hyatt (1998b, 2004) records 130 taxa for Arkansas; many of these occur only in the mountainous regions of the northwestern half of Arkansas. Anton A. Reznicek (pers. comm.) reports that some Michigan counties have more than 100 taxa. For other states, a review of *Carex* distribution in Kartesz (1999) demonstrates the north-to-south decrease in number of *Carex* taxa. He lists the following number of *Carex* taxa per state, with the states generally listed north to south, but organized here by number of documented taxa from high to low: Tennessee, 147; Missouri, 133; Kentucky, 121; Alabama, 118; Mississippi, 100; Oklahoma, 95; Texas, 93; Louisiana, 75. Based on field experience and on distributions from Thomas and Allen (1993a), a few additional *Carex* taxa could occur on the Forest, including *C. comosa* Boott, *C. lupuliformis* Sartwell ex Dewey, and *C. ozarkana* P. E. Rothr. & Reznicek.

Most *Carex* species of the Forest are globally secure. *Carex decomposita*, at G3, is the rarest globally rare species. State frequency information for most species, which can be used for the production of S ranks, is being submitted to NatureServe.

Acknowledgments

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Figure 7. *Carex socialis* to *C. venusta* collection sites, and locations for all collections.

Reznicek graciously provided assistance with plant identification. Herbarium loans were provided by LAF, LSU, LTU, NATC, and NLU.

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Chapter 5

Description of the Population, Canopy Cover, and Associated Vegetation of the Globally Rare Sedge *Carex polymorpha* (Cyperaceae) in Nescopeck State Park, Pennsylvania

Jamie L. Horvath, Timothy A. Block, and Ann Fowler Rhoads

ABSTRACT *Carex polymorpha* Muhl. (variable sedge) is a globally rare sedge ranging from Maine to West Virginia, with one of the largest known populations in Nescopeck State Park, Pennsylvania. As a first step in describing the Nescopeck population and its habitat, 30 plots were established during the fall of 2001 to (1) estimate the abundance and flowering percentage of *C. polymorpha*, (2) estimate percent canopy closure, (3) characterize the associated vegetation, and (4) make management suggestions to Nescopeck State Park. The number of vegetative *C. polymorpha* shoots ranged from 1–183 shoots • m^{-2} and averaged 35.5 shoots • m^{-2}. Eight of 60 1-m^2 quadrats contained flowering shoots, and the ratio of flowering to vegetative shoots was 1:193 (0.52% flowering). Canopy closure ranged from 63.8%–89.8% and averaged 83.3%. In Nescopeck, *C. polymorpha* grows in a plant community best described as dry oak–heath forest. Abundant canopy species included *Quercus alba* L., *Acer rubrum* L., and *Amelanchier arborea* (F. Michx.) Fernald. Ericaceous shrubs were abundant in the understory, and the two most abundant herbs were *Gaultheria procumbens* L. and *Rubus hispidus* L. Cluster analysis did not reveal a specific vegetation association in which flowering shoots of *C. polymorpha* grouped. The lack of a clear pattern suggests that factors other than the associated vegetation, i.e., hydrology, soil characteristics, and microsite light levels, may be influencing *C. polymorpha*, and future research should explore this hypothesis. We recommend defining current population boundaries and establishing permanent plots in order to monitor *C. polymorpha* in Nescopeck. Transects that run through areas with *C. polymorpha*, as well as surrounding areas without, is a logical second step to characterizing the habitat of *C. polymorpha* at Nescopeck.

KEY WORDS Associated vegetation, *Carex polymorpha*, flowering percentage, globally rare species, Nescopeck State Park, percent canopy closure.

Carex polymorpha Muhl. (variable sedge) is a globally rare sedge that ranges from Maine to West Virginia (Fig. 1). Its global rank is Vulnerable (G3; NatureServe, 2005) and nine of 12 states list *C. polymorpha* as either Endangered or Threatened (USDA, 2004). The largest threat to *C. polymorpha* is habitat destruction. Populations have been subject to sand and gravel mining, residential and vacation home development, topsoil removal, and development of lowland areas for cranberry production (Standley & Dudley, 1989; Rawinski & Sneddon, 1991; NatureServe, 2005).

Carex polymorpha is a perennial, rhizomatous herb that produces annual shoots. Individual shoots can remain vegetative during the growing season or may bear a single fertile culm with multiple spikes. Vegetative shoots grow to 40 cm in height with leaf blades 2.5–6 mm wide. Leaves are a pale green color, changing to tawny yellow in mid-September or October. The lower sheaths of *C. polymorpha* are bladeless and brown to red-purple tinged (Standley & Dudley, 1989; Rhoads & Block, 2000).

Sexually reproducing *Carex polymorpha* shoots grow to 60 cm in height, bearing 1–3 staminate spikes terminally and (0)1–2(3) pistillate spikes laterally, some of which are staminate distally (Standley & Dudley, 1989; Rhoads & Block, 2000). Flowering phenology begins with an initial pistillate phase that lasts less than a week, followed by a hermaphroditic phase for one to two days, ending with a staminate phase that lasts from one to several days. Achenes mature approximately eight weeks after flowering (Standley & Dudley, 1991). *Carex polymorpha* appears to be self-compatible and is not apomictic (Standley & Dudley, 1991).

The perigynia of *Carex polymorpha* are 4–5.5 × 1.5–2.5 mm in size, green to light brown, with low broad papillae (Rhoads & Block, 2000). The perigynia have long beaks (1–2 mm) that are purple-tinged with an oblique, hyaline orifice (Rhoads & Block, 2000), and they are densely arranged on the pistillate spikes in three or more rows (NatureServe, 2005).

Vegetative reproduction of *Carex polymorpha* through rhizomatous growth (Fig. 2) is sympodial. Development of elongate rhizomes results in a growth pattern of single, isolated shoots; development of short, ascending rhizomes results in clusters of shoots. Within a square meter, however, relatively few shoots belong to the same clone, suggesting the existence of a high level of competition among different genets (Standley & Dudley, 1991).

In 1991, Standley et al. conducted a study to determine the genetic variability of *Carex polymorpha*, comparing it to the common *C. vestita* Willd., a sympatric and morphologically similar sedge. The results indicated that the genetic diversity of *C. polymorpha* is comparable to that of *C. vestita* and, more importantly, that there is no correlation between rarity and genetic variation in *C. polymorpha*. Standley et al. (1991) place *C. polymorpha* in a group of rare endemic species that: (1) maintain a significant level of variation, (2) have numerous polymorphic loci, and (3) have high levels of within- or among-population variation. As a result, *C. polymorpha* is likely to respond to environmental changes and is not in immediate danger of extinction due to genetics (Standley et al., 1991).

Carex polymorpha populations vary in size and density (Fleming, 1985; Standley & Dudley, 1989; Everett, 2001). Populations range from fewer than 100 shoots to a million shoots (Standley & Dudley, 1989; Everett, 2001). *Carex polymorpha* also grows in a variety of habitats. Elevations of populations range from close to sea level in New England to above 1250 m on Panther Knob, West Virginia (Fleming, 1985; Everett, 2001). *Carex polymorpha* is classified as a facultative upland species (USFWS, 1997); however, it is also described as growing in buffer zones of wetlands and occasionally sphagnum (Standley & Dudley, 1989; Rawinski & Sneddon, 1991).

Carex polymorpha grows in several vegetation types, including forest, woodland, scrub, and edge habitat (e.g., railroad lines, utility right-of-ways) (Standley & Dudley, 1989; Rawinski & Sneddon, 1991). Associated species vary, but common canopy associates include oaks (*Quercus rubra* L., *Q. ilicifolia* Wangenh.), pines (*Pinus rigida* Mill., *P. strobus* L.), and red maple (*Acer rubrum* L.). The understory is often dominated by ericaceous shrubs such as black huckleberry (*Gaylussacia baccata* (Wangenh.) K. Koch), blueberry (*Vaccinium angustifolium* Aiton, *V. corymbosum* L.), mountain laurel (*Kalmia latifolia* L.), and teaberry (*Gaultheria procumbens* L.) (Rawinski & Sneddon, 1991).

Carex polymorpha is often found in sandy friable soils that allow for the movement and growth of rhizomes (Rawinski & Sneddon, 1991). Soils are

Figure 1. The global range of *Carex polymorpha* is limited to the northeastern United States, ranging from Maine to West Virginia. Nine states list *C. polymorpha* as either endangered or threatened (USDA, 2004). Inset: gray = endangered; black = threatened; stippled = endangered, extirpated; white = not listed; striped = no recorded occurrences.

also considered highly acidic and oligotrophic, and the organic layer can be completely absent to thick (Standley & Dudley, 1989). It has been suggested that *C. polymorpha* colonizes naturally disturbed soils; *C. polymorpha* grows in some areas that are prone to fire, and probably withstands or is even enhanced by fire (Rawinski & Sneddon, 1991).

Standley and Dudley (1991) explored the relationship between canopy closure and the growth and reproduction of *Carex polymorpha*. Their results indicated that *C. polymorpha* is limited by light availability. The density of shoots, the number of achenes produced, and the percent seed-set were all significantly higher in open sites. A correlation between the number of flowering shoots and canopy closure was also suggested, such that canopy cover < 50% promotes flowering, 50%–80% limits flowering, and > 80% inhibits flowering completely.

Nescopeck State Park in northeastern Pennsylvania contains one of the largest known populations of *Carex polymorpha* (Fig. 3). As a first step in describing the Nescopeck population and its habitat, a study was conducted to: (1) estimate the abundance and flowering percentage of *C. polymorpha*, (2) estimate percent canopy closure, (3) characterize the associated vegetation, and (4) make management suggestions to Nescopeck State Park.

METHODS

SITE DESCRIPTION

Nescopeck State Park is a 1262-ha. state park located in Dennison and Butler Townships, Luzerne County, Pennsylvania (park office 41°37′N, 75°53′W). The average high temperature in July is 20°C and the average low temperature in January is –4°C. Average annual precipitation is 1.19 m in the forms of rain, fog, and snow. Flood conditions occur at least once a year (DCNR, 2001).

Nescopeck State Park is part of the Ridge and Valley physiographic province of the Appalachian Mountain section (Braun, 1950) and lies within

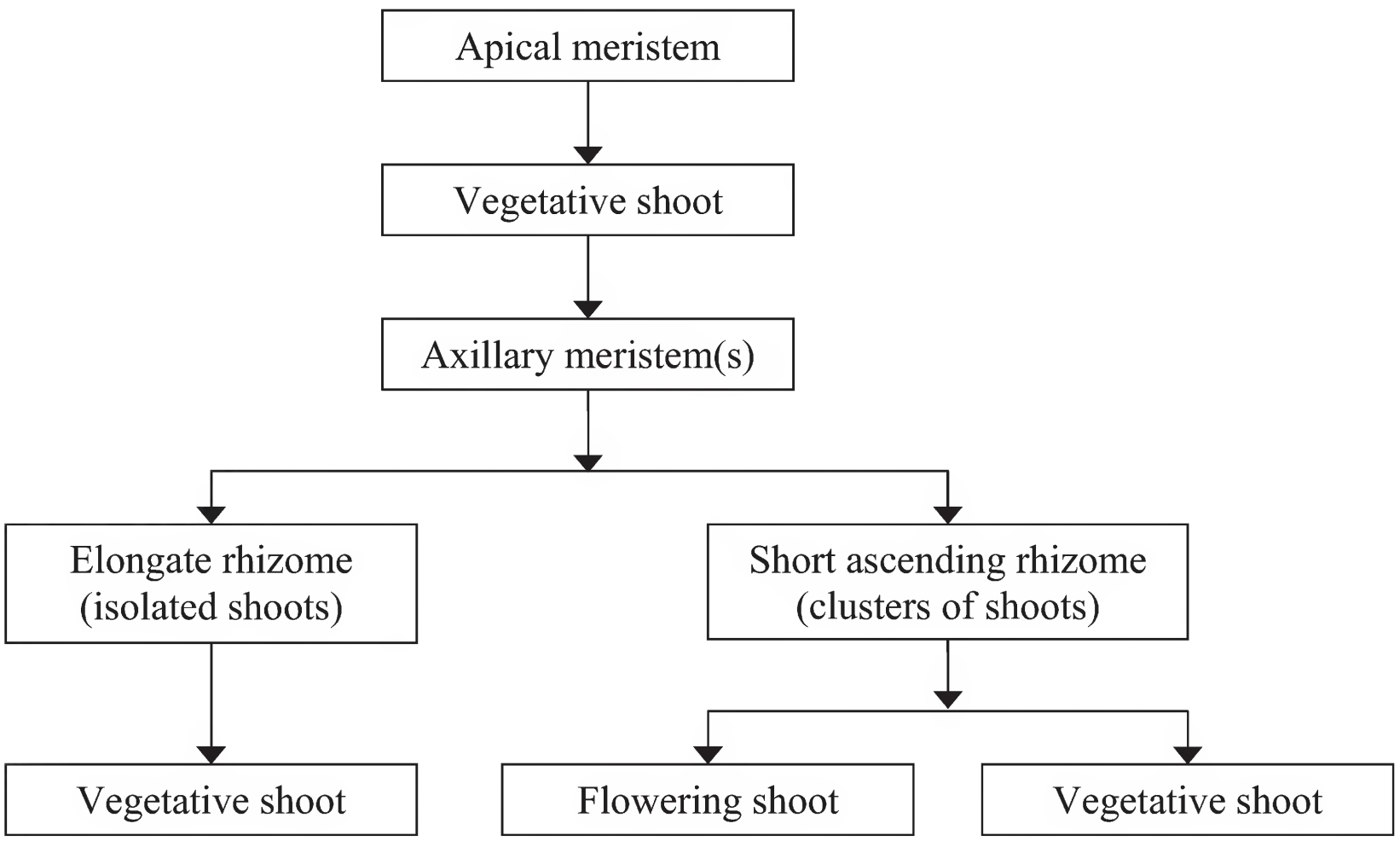

Figure 2. The vegetative reproduction of *Carex polymorpha* through rhizomes is sympodial. Growth pattern is determined by the development of two types of rhizomes (1) elongate rhizomes producing a pattern of single, isolated shoots or (2) short ascending rhizomes producing clusters of shoots.

Nescopeck Valley. The valley is flanked by Nescopeck Mountain (elevation 501 m) to the north and Mount Yeager (elevation 585 m) to the south, and the elevation within the park ranges from 314–408 m (DCNR, 2001). Nescopeck Creek flows east to west through the park, eventually meeting the north branch of the Susquehanna River in central Pennsylvania.

The bedrock of Nescopeck State Park belongs to the Mississippian Age Mauch Chunk formation and is a complex of shales, mudstone, sandstone, and conglomeratic sandstone (DCNR, 2001). This bedrock is covered by a mixture of glacial, glaciofluvial, and alluvial sediments (DCNR, 2001).

Nescopeck State Park is surrounded almost entirely by State Gamelands 187; as a result, the majority of the valley is forested land and supports a variety of plant communities. The south-facing slope of Nescopeck Mountain is dominated by oak forest, while the north-facing slope of Mount Yeager is composed of northern hardwood forest. In the valley along Nescopeck Creek, there is a network of several plant communities occurring in small patches. Included in the network are areas of hemlock forest, early successional fields, and wetlands (Rhoads & Block, unpubl. data).

Nescopeck Valley has been impacted by humans in a variety of ways in recent history (DCNR, 2001). During pre-colonial time, the valley was part of the range of the Native American Lenni Lenape, and may have been utilized by the neighboring Susquehannock. The Lehigh Path also passed through Nescopeck Valley, heading north to the town of Wyoming; both Native Americans and European colonists traveled along this passage during the seventeenth and eighteenth centuries. In the 1800s, heavy timbering of *Pinus strobus* (eastern white pine) and *Tsuga canadensis* (L.) Carrière (Canada hemlock) occurred, and sawmills were built along Nescopeck Creek. In the latter half of the century, there was a decline in the timber industry and the valley shifted to agriculture. By the early 1900s, small dairy farms were established. The land, however, was not extremely productive, and by the

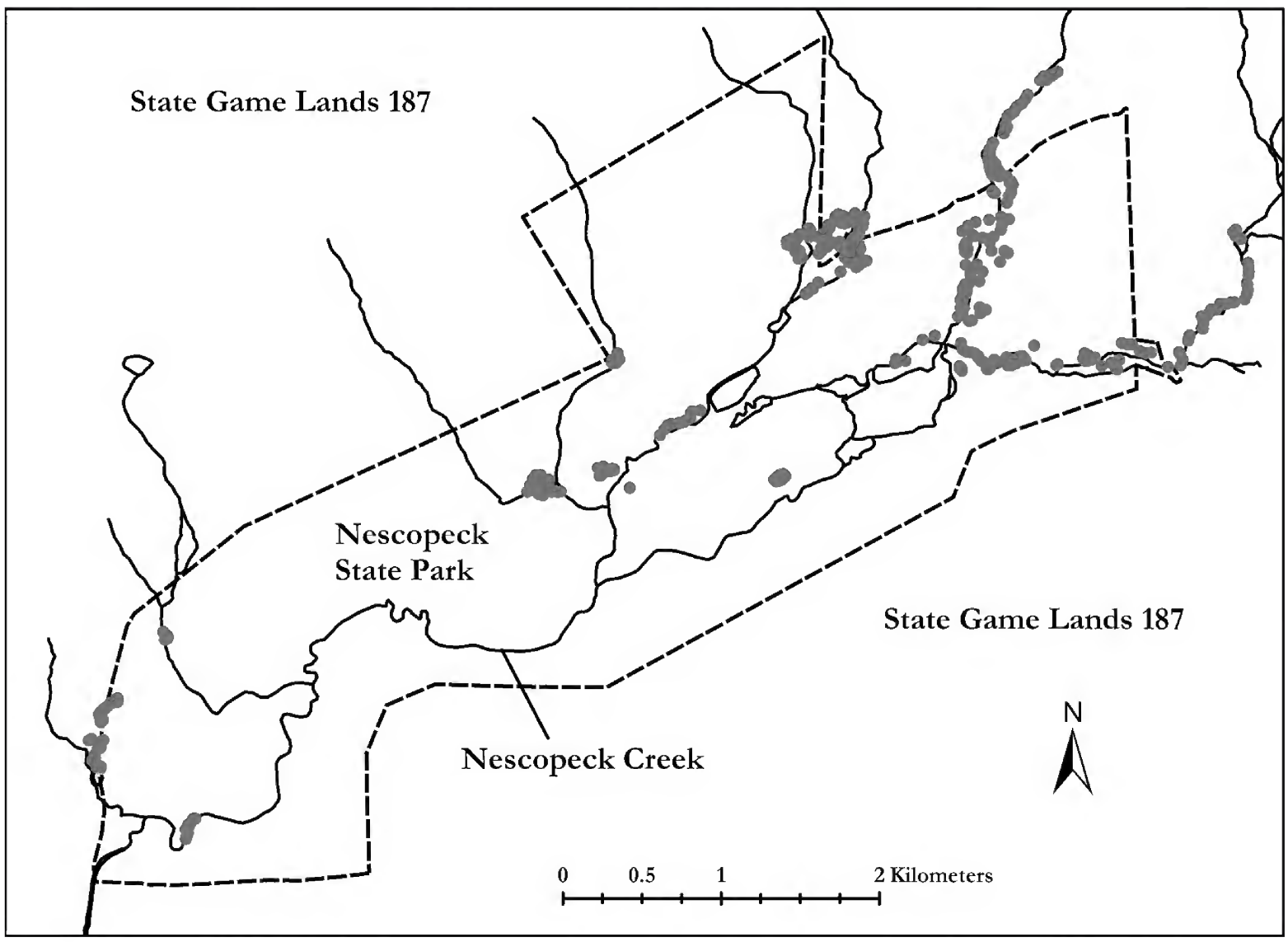

Figure 3. Distribution of *Carex polymorpha* in Nescopeck State Park and State Gamelands 187. Dashed lines indicate the park boundary, solid lines are streams, and circles represent presence of *C. polymorpha*.

1950s, the valley was used for business and industry. Examples include a stone quarry, sand pit, nursing home, and small housing developments. In the 1960s, the first steps were taken to establish a state park in the region, and today Nescopeck Valley is used primarily for recreation.

PLOT ESTABLISHMENT

The populations of *Carex polymorpha* in Nescopeck State Park and State Gamelands 187 were mapped using ArcView GIS 3.2 prior to this study (Environmental Systems Research Institute, Inc., 1999; Rhoads & Block, unpubl. data). We established thirty 10 × 10-m plots in the mapped areas containing *C. polymorpha* (Fig. 3). A 2 × 2-m grid divided into four equal 1 × 1-m quadrats was nested in each plot. The location of each grid was randomly chosen, with the single criterion that it must contain *C. polymorpha*. The distribution of *C. polymorpha* within the four quadrats, however, was not dictated.

DATA COLLECTION AND CALCULATIONS

Data were collected from 8 September–1 October 2001. We counted the number of flowering and vegetative *Carex polymorpha* shoots in two randomly chosen 1 × 1-m quadrats within the grid to determine the abundance of *C. polymorpha* per quadrat and per plot. All 60 quadrats (2 quadrats × 30 plots) were combined to calculate the ratio of flowering to vegetative shoots and the flowering percentage at Nescopeck.

Percent canopy closure per plot was estimated using a digital camera (Olympus Camedia C-2500L). An image of the canopy was taken with a standard 35-mm lens directly above each plot corner (camera height = 0.5 m) from 24 August–5 September 2001. Images were taken 10 m apart, such that there was no overlap in their aerial coverage. Using Image Tool for Windows Version 2.02 (Wilcox et al., 1999), we converted each color image to black and white, and counted the black and white

pixels. The percentage of black pixels in an image represented the percent canopy closure for that plot corner. Percent canopy closure for an entire plot was calculated by averaging the percent canopy closures of its four corners. A regression was run to determine if percent canopy closure could predict the total number of *Carex polymorpha* shoots • plot^{-1}.

The vegetation associated with *Carex polymorpha* in each plot was divided into three layers: canopy, understory, and herbaceous. Canopy vegetation included all woody trees and shrubs 1 m or taller within the 10 × 10-m plot. The species name and diameter at breast height (DBH = 1.3 m) were recorded for all individuals ≥ 1.3 m tall. The diameter of an individual shorter than breast height (≥ 1.0 m and < 1.3 m) was measured at the highest point on the individual. Basal area was calculated for each individual and summed by species for basal area • species^{-1} • plot^{-1}. Understory vegetation included all woody trees and shrubs less than 1 m tall within the 2 × 2-m grid. Tree seedlings were included in the understory. The percent cover of each understory species was estimated visually in all four 1 × 1-m quadrats. Percent cover was estimated at 5% increments from 0%–100%. The average percent cover of the four quadrats was calculated by species to determine the percent cover • species^{-1} • plot^{-1}.

Herbaceous vegetation included all herbaceous species in the two 1 × 1-m quadrats in which *Carex polymorpha* shoots were counted (see above). Woody perennial species with creeping habits, e.g., *Gaultheria procumbens*, *Rubus hispidus* L. (swamp dewberry), and *Epigaea repens* L. (trailing-arbutus), were included in the herbaceous vegetation. Percent cover for each species was estimated visually using the same method described for the understory vegetation. The percent cover of the two quadrats was averaged by species to determine the percent cover • species^{-1} • plot^{-1}.

CLUSTER ANALYSIS

Cluster analysis was used to determine if the habitat of *Carex polymorpha* was characterized by a particular vegetation association(s). We were interested in the similarity in vegetation among plots, and therefore used a grouping technique rather than ordination (McCune & Mefford, 1999). A plot-by-species matrix was constructed for each layer. Where two species in the same genus were present and one was present in only a single plot, the two species were combined and classified at the generic level. The herbaceous (30 plots × 30 species) and understory (30 plots × 24 species) matrices contained relative cover • plot^{-1} • species^{-1}; the canopy matrix (30 plots × 23 species) contained relative basal area • plot^{-1} • species^{-1}. A plot-by-layer matrix (30 plots × 3 layers) was also constructed using total cover • plot^{-1} (sum of all species) for the herbaceous and understory layers and percent canopy cover • plot^{-1} for the canopy. Cluster analysis was performed with PC-Ord for Windows Version 4.25 (McCune & Mefford, 1999) using the Sorensen (Bray-Curtis) distance measure and the Group Average linkage method.

RESULTS

ABUNDANCE OF *CAREX POLYMORPHA* SHOOTS

The number of vegetative shoots of *Carex polymorpha* ranged from 1–183 shoots • m^{-2}. A total of 2130 shoots (vegetative and flowering) were counted in the 60 quadrats, with an average of 35.5 shoots • m^{-2} (median = 27 shoots • m^{-2}). Only eight quadrats in eight separate plots contained flowering shoots. The number of flowering shoots ranged from 0–3 shoots • quadrat^{-1}, and the median percentage of flowering shoots • quadrat^{-1} was 2.0%. The ratio of flowering to vegetative shoots in Nescopeck Valley was 1:193 and the percent flowering was 0.52%.

PERCENT CANOPY CLOSURE

The canopy closure per plot ranged from 63.8%–89.8% with an average of 83.3%. Percent canopy closure explained 43% of the variation in the total number of *Carex polymorpha* shoots per plot ($R^2 = 0.426$), and only six plots had a canopy closure < 80%. The average canopy closure for the eight plots with flowering shoots was 80.6%. The average canopy closure for the 22 plots without flowering shoots was 84.2%.

ASSOCIATED VEGETATION

Seventy-three plant species were associated with *Carex polymorpha* at Nescopeck. *Carex polymorpha* populations are typically located near a stream or water source in Nescopeck (Block & Rhoads, pers. obs.), and 61 of the 73 species (84%) were listed as wetland plants by the U.S. Fish and

Wildlife Service (USFWS, 1997). Of those species listed by the USFWS, 52% were designated as facultative upland (FACU) or upland species (UPL) with only a 1%–33% chance of occurring in a wetland (USFWS, 1997).

The most abundant canopy species was *Quercus alba* L. (white oak), which was one of the three most abundant canopy species in 25 of 30 plots. Other abundant canopy species were *Acer rubrum*, *Amelanchier arborea* (F. Michx.) Fernald (shadbush), and *Hamamelis virginiana* L. (witch hazel). In 18 of 30 plots, ericaceous species such as *Vaccinium angustifolium* (low sweet blueberry), *Gaylussacia baccata*, *Kalmia angustifolia* L. (sheep laurel), and *Rhododendron periclymenoides* (Michx.) Shinners (pinxter flower) were most abundant in the understory. *Amelanchier arborea* and *Q. rubra* (red oak) were also abundant in the understory. The herbaceous vegetation was slightly more diverse than the canopy and understory, with 34 different species compared to 27 and 29 species, respectively. The two most abundant herbaceous species were *Gaultheria procumbens* and *Rubus hispidus*.

Cluster analysis of the canopy vegetation revealed two predominant clusters and five outliers (Fig. 4). Cluster A (n = 7 plots) contained > 33% *Acer rubrum* and < 50% *Quercus alba*, while cluster B (n = 18) contained < 33% *A. rubrum* and > 50% *Q. alba*. Four of the five outliers contained pine (*Pinus rigida* or *P. strobus*) while clusters A and B did not. Three of the eight plots with flowering shoots were grouped in cluster A, four plots in cluster B, and one plot was an outlier (Fig. 4).

While retaining 62.5% of the information in the clusters, the herbaceous vegetation produced six clusters with four outliers, and the understory vegetation produced eight clusters with four outliers (Figs. 5 and 6). In both the herbaceous and understory layers, plots with flowering shoots were scattered among the different clusters.

Cluster analysis of the cover • plot^{-1} for the three layers produced two main clusters (Fig. 7). Cluster A (n = 18) had a total understory cover (for all species) between 125% and 235% and cluster B (n = 12) had a total understory cover of 265%–505%. Five of the eight plots with reproducing shoots were grouped in cluster A, and the remaining three plots were grouped in cluster B.

Discussion

The population of *Carex polymorpha* at Panther Knob, West Virginia, is considered the largest in the world (NatureServe, 2005). In the dwarf pine forest, there was an average of 404 shoots • 100 m^{-2} (range 10 to 3500 shoots). In the dwarf red oak forest, *C. polymorpha* was even more abundant, averaging 6333 shoots • 100 m^{-2} (range 1000 to 15,000 shoots) (Fleming, 1985). Estimates of *C. polymorpha* at Nescopeck fall between the two forest types on Panther Knob, averaging 3550 shoots • 100 m^{-2} (range 300 to 13,300 shoots).

Sexual reproduction of *Carex polymorpha* at Nescopeck is extremely low, with a ratio of flowering to vegetative shoots of 1:193 (0.52% flowering). Past studies conducted on populations of *C. polymorpha* have also revealed low levels of flowering. In Maine, the percentage of flowering shoots ranged from 0%–1.5% (Standley & Dudley, 1991). On Panther Knob, the ratio of flowering to vegetative shoots was 1:127 with less than 1% flowering (Fleming, 1985). This pattern fits the strategy of many other herbaceous perennials that maintain populations with vegetative growth and allocate resources to sexual reproduction only under favorable environmental conditions (Standley & Dudley, 1991).

Percent canopy closure associated with *Carex polymorpha* at Nescopeck was high. The canopy closure averaged 83.3%, ranging from 63.8%–89.8%. Comparable canopy closure of 65%–80% in Falmouth Woods, Maine, and Duxbury, Massachusetts, was also considered high in relation to other populations studied by Standley and Dudley (1991). They suggested that < 50% canopy closure promotes flowering, 50%–80% limits flowering, and > 80% completely inhibits flowering. Only six plots in Nescopeck had a canopy closure < 80%, half of which had flowering shoots. Calculating the percent canopy cover separately for flowering and non-flowering plots in Nescopeck produced an average canopy cover of 80.6% (n = 8) and 84.2% (n = 22), respectively. These two values fall in line with the parameters established by Standley and Dudley (1991).

Standley and Dudley (1991) found that the density of *Carex polymorpha* shoots was correlated to canopy closure, with a higher density of shoots occurring in more open sites. Percent canopy closure

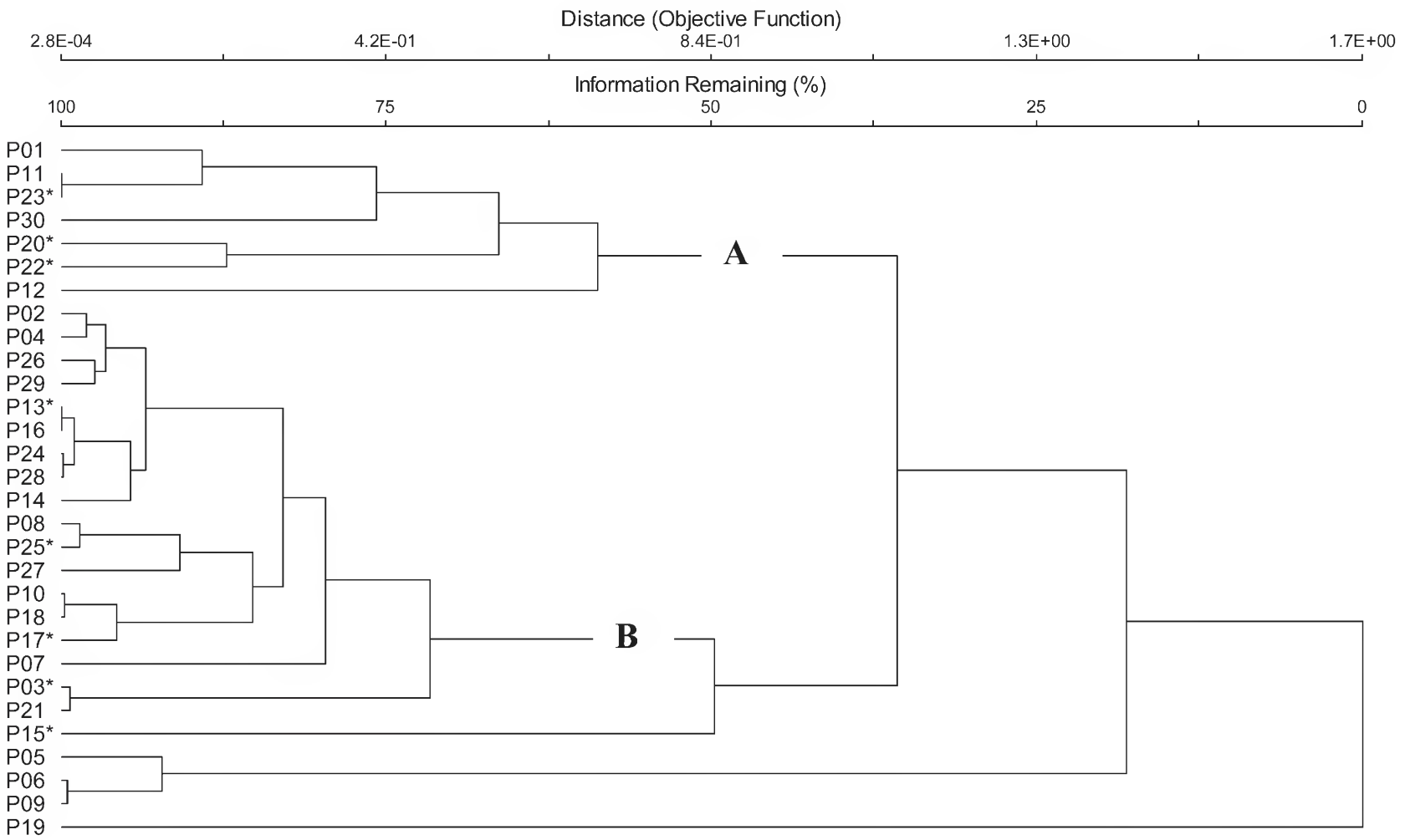

Figure 4. Cluster dendrogram for the canopy vegetation associated with *Carex polymorpha*. Cluster analysis is based on the relative basal area • species^{-1} • plot^{-1}. Plots in cluster A (n = 7) had > 33% *Acer rubrum* and < 50% *Quercus alba*; plots in cluster B (n = 18) had < 33% *A. rubrum* and > 50% *Q. alba*. Five outliers were not part of clusters A and B, four of which contained pine. Plots with an asterisk (*) contained flowering shoots.

explained 43% of the variation in shoot abundance in Nescopeck (R^2 = 0.426), such that greater canopy cover predicts fewer *C. polymorpha* shoots. The percent canopy closure at Nescopeck covered a smaller range (26%) than Standley and Dudley's (1991) three categories of cover, perhaps masking a stronger relationship.

A more accurate estimate of canopy closure or light penetration, particularly at the microenvironment level, may produce a stronger relationship with shoot abundance. In Plot 20, a portion of the plot was an abandoned road that had become revegetated, but had little or no canopy. The remainder of the plot was vegetated with a developed canopy. As a result, the percent canopy closure produced an average of the two distinctly different canopies (63.8%). More importantly, the two quadrats sampled for number of *Carex polymorpha* shoots were in the abandoned road with a completely open canopy. Shoot abundance in the two quadrats was the highest at Nescopeck, and Plot 20 was one of eight plots with flowering shoots. This example illustrates the need for better measures of canopy closure or light penetration at a more appropriate scale for *C. polymorpha*.

In Nescopeck, *Carex polymorpha* grows in a plant community best described as dry oak–heath forest (Fike, 1999). *Quercus alba* was the most abundant tree species and the understory had an abundance of ericaceous shrubs. Cluster analysis of the canopy vegetation (Fig. 4) produced two main clusters that were dominated by either *Q. alba* or *Acer rubrum*, lending more support to this community classification. Cluster analysis of the herbaceous and understory vegetation did not reveal any clear patterns to aide in classification.

Evidence suggests that *Carex polymorpha* inhabits both moderately wet and dry sites in Nescopeck, with a tendency toward dry sites. Eighty-four percent of the species associated with *C. polymorpha* are listed as wetland plants (USFWS, 1997), but half of those plants are considered facultative upland or upland species. In addition, dry oak–heath forest occurs on xeric to moderately dry sites (Fike, 1999). The cluster analysis of the canopy vegetation (Fig. 4) produced

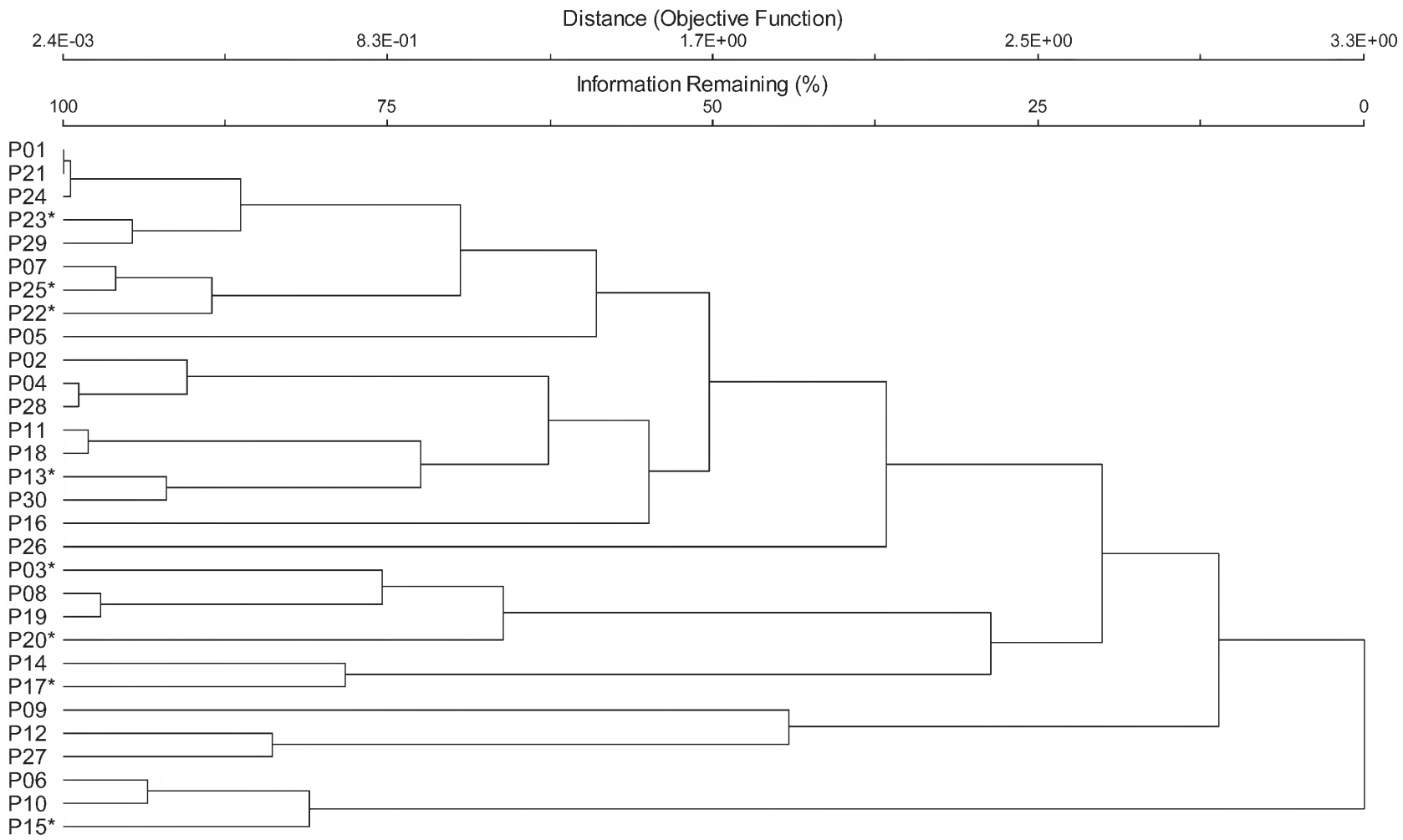

Figure 5. Cluster dendrogram for the herbaceous vegetation associated with *Carex polymorpha*. Cluster analysis is based on relative cover • species^{-1} • plot^{-1}. Plots with an asterisk (*) contained flowering shoots.

two clusters that differed in their proportions of *Quercus alba* and *Acer rubrum*. Considering that *Q. alba* inhabits drier sites and *A. rubrum* is associated with wetter sites, a greater number of plots (n = 18; *Q. alba* > 50%; *A. rubrum* < 33%) were most likely dry sites, while fewer sites (n = 7; *Q. alba* < 50%; *A. rubrum* > 33%) were wetter.

The cluster dendrograms for the three vegetation layers (Figs. 4–6) illustrate that there is no apparent relationship between a particular vegetation type and the presence of flowering shoots of *Carex polymorpha*. Plots with flowering shoots do not group together within any clusters, and they also appear as outliers in the understory and canopy analyses. The cluster dendrogram for the total cover • plot^{-1} of the three layers (Fig. 7) reveals two clusters that varied in the amount of understory vegetation; however, the presence of flowering shoots did not relate to the two clusters. This analysis suggests that neither the associated species nor the total vegetation cover relates to the flowering of *C. polymorpha*. Future research should explore different environmental factors that may affect flowering, i.e., hydrology, soil characteristics, and microsite light levels.

The variation in community type at Nescopeck fits the growth pattern for *Carex polymorpha*. Standley and Dudley (1989) surveyed populations in six states (Maine, Massachusetts, Pennsylvania, New Hampshire, Rhode Island, and Connecticut) and concluded that there was considerable variation in the dominant community type at the sites. On Panther Knob, Fleming (1985) identified regular associates of *C. polymorpha*, but noted that many other species could be added to the list. In New England and Panther Knob, no single species was considered an indicator for growth of *C. polymorpha* (Fleming, 1985; Everett, 2001).

The lack of a specific vegetation type associated with *Carex polymorpha* could be a function of scale as well as a function of environmental factors. *Carex polymorpha* may be more limited by its microenvironment, which would account for adaptability to a variety of vegetation types. This idea is supported by the fact that the rhizomatous growth pattern of *C. polymorpha* facilitates exploitation of favorable microsites (Standley & Dudley, 1989). Rhizome growth and shoot production presumably occur in response to nutrient and energy gradients

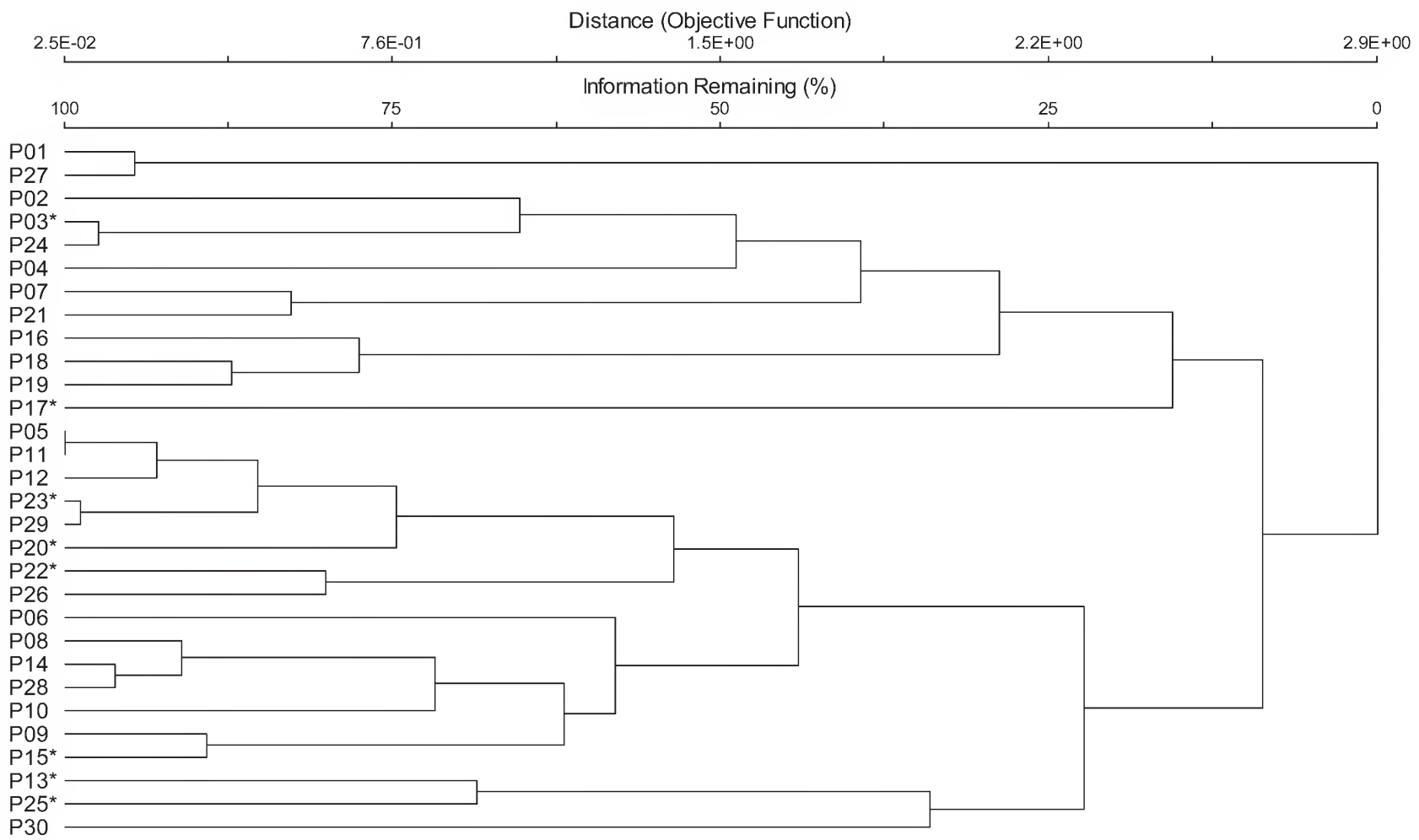

Figure 6. Cluster dendrogram for the understory vegetation associated with *Carex polymorpha*. Cluster analysis is based on relative cover • species^{-1} • plot^{-1}. Plots with an asterisk (*) contained flowering shoots.

(Standley & Dudley, 1989). Fleming (1985) found that *C. polymorpha* colonized openings in the heath layer on Panther Knob. This pattern could result from the lack of competition at the microsite level rather than from the associated vegetation type.

If habitat destruction is the major threat to *Carex polymorpha*, the populations in Nescopeck are not in immediate danger. Yet, even with protection of the land, the loss of suitable habitat for *C. polymorpha* is still a concern. Everett (2001) theorizes that *C. polymorpha* persists vegetatively in forests prone to fire and storm damage. After a disturbance creates a canopy gap, conditions are more favorable for *C. polymorpha* and it allocates significant resources to sexual reproduction. This burst of sexual reproduction is thought to facilitate rapid expansion of *C. polymorpha* populations, an expansion that could be limited today by habitat fragmentation and fire suppression (Everett, 2001).

The communities at Nescopeck have experienced some disturbance over time. On the regional scale, the forests of eastern Pennsylvania are recovering from the loss of the canopy species *Castanea dentata* (Marshall) Borkh. (American chestnut) to the chestnut blight (Braun, 1950). On a more local scale, Nescopeck Valley has been utilized for centuries, beginning with the Lenni Lenape in pre-colonial times (DCNR, 2001). It is possible that the Lenni Lenape used fire to manage the forests. Fire-tolerant species such as *Pinus rigida*, *Quercus ilicifolia*, and ericaceous shrubs persist. Currently fire is suppressed in the park, but recreational trails maintain edge habitat, and storms provide local disturbance.

In order to ensure the maintenance of suitable habitat for *Carex polymorpha* at Nescopeck, it would be prudent to establish a monitoring program at the park. Standley and Dudley (1989) describe a protocol of defining population boundaries and conducting annual surveys of those boundaries to determine if populations are expanding or declining. In addition, shoot density is monitored annually in permanent plots (Standley & Dudley, 1989), recording the number of flowering and vegetative shoots. The 60 quadrats established in this study and the map of *C. polymorpha* in Nescopeck Valley provide initial data to launch a monitoring program.

The data collected on the abundance of associated vegetation could also be used to monitor the rate

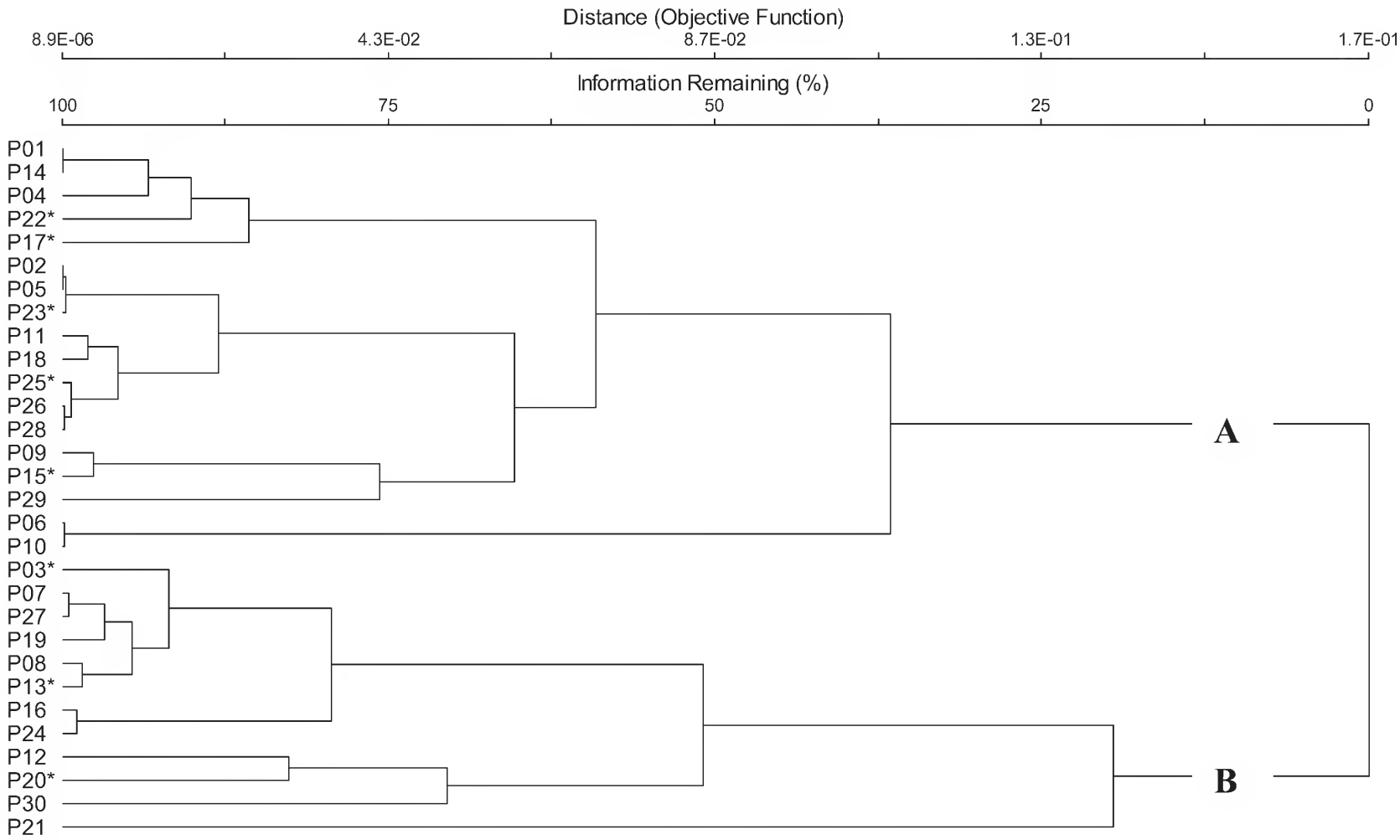

Figure 7. Cluster dendrogram using the total cover • plot^{-1} of the herbaceous and understory layers, and percent canopy cover • plot^{-1} to group similar plots. Cluster A (n = 18) had a total understory cover (for all species) of 125%–235%, while cluster B (n = 12) had a total understory cover of 265%–505%. Plots with an asterisk (*) contained flowering shoots.

of succession at Nescopeck. The percent canopy closure and competition with understory and herbaceous vegetation could be affecting the growth of *Carex polymorpha* (Fleming, 1985; Standley & Dudley, 1991). Removal of understory shrubs and small trees could be a management strategy. In Maine, Woodlot Alternatives, Inc. (1998) removed woody vegetation with DBH < 4 inches in plots with both native and transplanted *C. polymorpha* and had mixed results. Peak years of growth and reproduction occurred one to two years after thinning of the understory, but were coupled with resprouting of stumps and, in some cases, increased competition in the understory (Woodlot Alternatives Inc., 1998). If the staff of Nescopeck State Park decides to actively manage the habitat of *C. polymorpha* in the future, substantial data will be needed prior to and following management activities to ensure that the desired results are obtained.

All plots in this study were placed in areas where *Carex polymorpha* was growing. Running transects through areas with and without *C. polymorpha* could provide useful insight into why this rare plant grows in some places but not others. Transects could also facilitate further exploration of environmental factors that affect the growth of *C. polymorpha*.

Conclusions

The population of *Carex polymorpha* at Nescopeck State Park is one of the largest in the world. Sexual reproduction is low, with only 0.52% of shoots flowering. Percent canopy closure at Nescopeck is high, ranging from 63.8%–89.8%, and could be inhibiting flowering. In Nescopeck, *C. polymorpha* is growing in a community type best described as dry oak–heath forest. Cluster analysis did not reveal a specific vegetation association in which flowering shoots of *C. polymorpha* grouped. Future research should explore environmental factors that could be influencing *C. polymorpha* distribution and flowering, including hydrology, soil characteristics, and microsite light levels. Sampling of transects through areas with and without *C. polymor-*

pha may also provide insight to its preferred habitat. A program should be established at Nescopeck to monitor population boundaries, shoot density, and flowering percentage.

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Chapter 6

Segregation of Sedge Species (Cyperaceae) Along Environmental Gradients in Fens of the Schefferville Region, Northern Quebec

Anna Dabros and Marcia J. Waterway

ABSTRACT Descriptive statistics, negative exponential surface plots, and canonical correspondence analysis were used to analyze distribution patterns of 27 sedge species along three environmental gradients: water pH, rooting position relative to water table, and distance to closest edge in 21 fens of the Schefferville region, northern Quebec. The occurrence and relative abundance of sedge species in each fen were recorded from 1609 quadrats (0.25 m^2) using stratified random sampling. The sedges of Schefferville fens segregated along the measured environmental gradients, with some species being more specialized along one or more gradients than others. All species had a narrow range of tolerance for rooting position relative to water table, but broader tolerances along pH and distance gradients. Species occupying similar positions along all three gradients tended to be distantly related, while more closely related species usually segregated on at least one of the gradients, suggesting niche partitioning.

KEY WORDS *Carex*, Cyperaceae, environmental gradients, *Eriophorum*, generalists, niche partitioning, peatlands, sedges, specialists, *Trichophorum*.

The large genus *Carex* L. (Cyperaceae), with more than 2000 species, can be found in a variety of temperate, boreal, and arctic habitats, including wetlands, forests, meadows, and tundra (Ball, 1990; Catling et al., 1990). Boreal and subarctic peatlands are rich in *Carex* species and other sedges, often with more than 25 species occurring within the same few hectares (Slack et al., 1980; Bubier, 1995). These open peatlands, often termed mires in the European literature (e.g., Sjörs, 1950; Malmer, 1986), support hydrophilic vegetation in poorly drained areas underlain by peat (Zoltai & Pollett, 1983). Environmental heterogeneity in mires is usually high, with variation in surface water flow, pH, nutrients, and microtopography. Diverse conditions can lead to high diversity of related species within plant communities—an issue addressed in equilibrium theories that emphasize niche partitioning among species, at least in part due to specialization along environmental gradients (Tilman, 1982; Tokeshi, 1999).

Traditionally, the ecological interpretation of mire plant communities has been based on Fennoscandian studies (Sjörs, 1950; Malmer, 1986) that define three major environmental gradients: (1) the poor-to-rich gradient, based on source of mineral supply to the peat surface, which divides mires into ombrotrophic bogs and minerotrophic fens; (2) the microtopography gradient, which determines height in relation to water table; and (3) the mire-margin to mire-expanse gradient, which stresses that mire margins receive more mineral-rich water than mire expanses. Different studies have emphasized different gradients as dominant with respect to plant distribution: poor-to-rich gradient (Vitt & Slack, 1975; Vitt et al., 1975; Vitt & Bayley, 1984; Gignac & Vitt, 1990; Glaser et al., 1990), microtopography gradient (Slack et al., 1980; Foster et al., 1988), or mire-margin to mire-expanse gradient (Cooper & Andrus, 1994; Anderson et al., 1996). However, it is becoming increasingly recognized that interplay among these and other environmental factors often results in complex gradients (Wheeler & Proctor, 2000; Økland et al., 2001; Risvold & Fonda, 2001; Bragazza & Gerdol, 2002). Wheeler and Proctor (2000), in a review of literature on ecological gradients in northwestern European mires, agreed that the water level or microtopography gradient is influential, but deemphasized the importance of a mire-margin to mire-expanse gradient. They also treated the poor-rich gradient as two distinct gradients: pH (base-poor vs. neutral or base-rich) and nutrient, citing N and P as limiting factors (Wheeler & Proctor, 2000).

The focus of many studies of peatland vegetation has been on defining plant communities in relation to these gradients, with sampling designed to characterize particular predefined microhabitats, including elevated areas such as hummocks and strings, and depressions such as pools and flarks (e.g., Slack et al., 1980; Foster et al., 1988; Bubier, 1995). This approach can bias interpretations of species' specific requirements and give an incomplete assessment of the full tolerance range for each species. In this study, we take a species-oriented approach, using stratified random sampling of a large number of quadrats throughout many mires with the goal of characterizing ecological preferences and tolerances of the suite of sedge species that occur in subarctic mires in eastern North America.

Sets of intrinsic traits, including morphology, physiology, life history, phenology, growth pattern and rate, resource requirements and use, and means of regeneration (dispersal, germination, and establishment), ultimately determine the ability of a plant species to persist under specific environmental conditions. Based on these traits, different species are expected to be associated with different optimal (micro)habitats, which consequently will be reflected in their distribution and abundance. While certain species (specialists) are more restricted in their distribution relative to environmental factors, other species (generalists) have wider tolerance levels (Colwell & Futuyma, 1971; Sultan et al., 1998).

The objective of this study was to characterize patterns of distribution and abundance for a diverse group of sedges that grow in subarctic peatlands with respect to the poor-rich gradient (indirectly measured by the water pH), the mire-margin to mire-expanse gradient (measured by the distance to the closest mire edge), and the microtopography gradient (measured by rooting position relative to water table). We assess whether this group of related species segregates along these gradients and whether their responses to these environmental factors are similar to those in other parts of their geographic ranges. We also investigate whether species with very similar environmental tolerances along the three gradients are closely or distantly related.

Materials and Methods

FIELD EXPERIMENTAL AREA

The study was conducted in the Schefferville area (54°47′N, 66°50′W), located within a geologically diverse region known as the Labrador Trough (Dimroth, 1972) in northern Quebec. Fens, which are mires receiving water inflow mainly from underground sources rather than strictly from precipitation, are the most common mire type in this area. They vary from minerotrophically rich fens, due to runoff from dolomitic substrates, to poor fens in areas with acidic bedrock. These fens exhibit microtopographic heterogeneity with low peat ridges (strings) alternating with water-filled depressions occupied by peat-forming vegetation (flarks), and often have pools of open water (Foster & King, 1984; Waterway et al., 1984; Foster et al., 1988). Dominant bryophytes in richer fens are brown mosses (Amblystegiaceae), *Tomenthypnum nitens* (Hedw.) Loeske, and a few *Sphagnum* L. species; different *Sphagnum* species dominate in poorer fens. At least 31 sedge species and two interspecific *Carex* hybrids occur in these fens, forming the dominant cover in many areas along with low shrubs including *Andromeda glaucophylla* Link, *Chamaedaphne calyculata* (L.) Moench., *Kalmia polifolia* Wangenh., *Ledum groenlandicum* Oeder, *Vaccinium uliginosum* L., *Potentilla fruticosa* L., *Betula pumila* L., and *Myrica gale* L. The fens generally have an open aspect with few tall trees (*Larix laricina* (Du Roi) K. Koch. and *Picea mariana* (Mill.) Britton, Sterns & Poggenb.) occupying islands or ridges within the fens. Smaller (usually less than 1.5 m tall) representatives of these tree species are scattered on fen margins.

SAMPLING DESIGN

Data on distribution patterns in relation to three environmental gradients were collected for 27 sedge species (21 *Carex*, four *Eriophorum* L., and two *Trichophorum* Pers.) from a total of 1609 square, 0.25 m^2 quadrats in fens of the Schefferville area (100,000 ha.) in the summer of 2001. The fens varied in shape and size from 0.25–19 ha., but were predominantly much longer than wide with heterogeneous microtopography including hummocks ranging from a few centimeters to a meter in height and pools often more than a meter in depth. Sampling was stratified in proportion to fen size across 21 fens and stratified within each fen by random sampling within each 5-m interval along five transects oriented perpendicular to the long axis of the fen. The location for each transect was randomly chosen within one of five equally spaced segments along the long axis of the fen, with length of segment dependent on fen length. For three small fens (less than 100 m long), only three transects were used. Within each quadrat, sedge species were identified and abundances were categorized by a modification of Braun-Blanquet's scale (Mueller-Dombois & Ellenberg, 1974): 0 for absence of species; 1 for < 5% abundance of species; 2 for 5%–25% abundance; 3 for 25%–75% abundance; 4 for > 75% abundance. To maintain consistency across quadrats, abundances were determined by consensus of the same three researchers throughout the summer. For each quadrat we also recorded water pH using a Sentron 10489 pH meter, distance (cm) from substrate where the plant was rooted either up (negative depth) or down (positive depth) to the water table using a meter stick, and distance (m) of each quadrat to the closest edge of the fen using a filometer to measure distance by metering the length of thread unraveled as a researcher walked. Variation in water depth and pH in these 0.25 m^2 quadrats was minimal so we recorded a single depth and pH value from the center of each quadrat. In quadrats without standing water, we dug into the hummock until we found the water table to make the measurements. Previous research in the area (M. J. Waterway, pers. obs.; T. R. Moore, McGill University, unpublished data) over the past 20 years indicates little variation in water level of these fens during the main growing season and little year-to-year variation.

STATISTICAL ANALYSIS

Means and standard deviations for rooting position in relation to water table (hereafter referred to as depth), water pH, and distance from nearest edge were calculated for each species from the quadrats in which each occurred. Box plots of depth, pH, and distance were created (StatSoft, Inc., 2001) for visualization of trends across species. The box represents values between the 25th and 75th percentiles while outliers and extreme outliers are defined as data values larger than the 75th percentile plus a coefficient multiplied by the width of the box, and data point

values smaller than the 25th percentile minus a coefficient multiplied by the width of the box. The coefficient was set to 1.5 for outliers, and 3 for extreme outliers. To assess differences in variability among species with different means, we calculated the ratio of standard deviation to mean (coefficient of variation, or CV hereafter) for depth, pH, and distance for each species. To avoid negative CVs, we rescaled all depth values by adding the overall most negative depth recorded, –65 cm, to each depth value collected. A relatively low CV for an environmental factor suggests a low range of tolerance for that factor (specialist species), while a high CV indicates a high range of tolerance for that factor (generalist species) but different sample sizes for each species must also be considered in interpreting CV values.

Exploratory surface plots were constructed using negative exponential smoothing to plot the abundance of each species against depth and pH (Statsoft, Inc., 2001). Negative exponential smoothing is a distance-weighted technique, in which a second degree polynomial is calculated for each value of the independent variable (depth and pH) to determine the response variable (abundance on a scale from 0 to 4), such that the influence of individual points decreases with distance from the particular independent variable value (StatSoft, Inc., 2001). In this case, distances were calculated according to a negative exponential function. These plots present a quick and useful visual indication of general trends in ecological preferences relative to depth and pH; however, mathematical extrapolations in the surface plots sometimes go beyond the boundaries specific for a particular study (e.g., negative abundances or abundances greater than four in this study). These extrapolations can be used to predict the optimal environmental conditions for species that may not be growing under optimum conditions in fens.

An ordination program, PC-ORD (McCune & Mefford, 1995), was used to perform canonical correspondence analysis (CCA) for the vegetation and environmental data from the 1609 sampled quadrats. For CCA, a multiple regression is performed at each iteration step of reciprocal averaging, which allows for selection of a linear combination of environmental variables that explain variation on each axis (ter Braak, 1986; Kent & Coker, 1992). As a direct gradient technique, CCA allows species composition to be directly related to measured environmental gradients (ter Braak, 1986). The gradient most strongly correlated with the first axis, which explains the highest percentage of variance, can be identified as the most influential in determining species' distributions. Results from the CCA ordination were plotted in two ways: as centroids of species scores to illustrate the distribution of species in relation to the environmental gradients, and as quadrat scores (weighted mean scores of the species in each quadrat) to illustrate the distribution of quadrats across the environmental space.

To assess overlap in species' occurrences along the environmental gradients, we calculated 95% confidence region ellipses (Sokal & Rohlf, 2003) for each species using ordination scores for all quadrats in which each particular species occurred, assuming that the first two axes of the CCA ordination follow a bivariate normal distribution. Species found in fewer than 50 quadrats were not included in these calculations. We overlaid these ellipses on the ordination diagram illustrating the distribution of quadrats, plotting each pair or group of *Carex* species in the same taxonomic section (Ball & Reznicek, 2002; Table 1) on the same graph to examine overlap. All ordination plots were created in STATISTICA (StatSoft, Inc., 2001) based on output from PC-ORD (McCune & Mefford, 1995).

Results

The 21 sampled fens varied from ca. 0.25 ha. to 19 ha. in size. We sampled 15–180 quadrats per fen and found 3–24 sedge species per fen, with a mean of 14 species. The length of transects varied from 15 to 245 m, averaging 50 m. There was a weak positive correlation between fen size and the number of sedge species found ($r^2 = 0.545$; $P < 0.05$). The number of species per 0.25 m^2 quadrat ranged from one to eight, with mean of 2.9 and median of 3. The mean number of quadrats in which any given species was found was 172.

Carex limosa L. was the most common species, found in 693 quadrats, while *C. aquatilis* Wahlenb. and *Trichophorum cespitosum* (L.) Hartm. were also found in more than 500 quadrats (Table 1). Two species (*C. saxatilis* L. and *Eriophorum vaginatum* L.) and two sterile hybrids (*C. limosa* × *rariflora* Norman and *C. limosa* × *magellanica* Figert) each occupied fewer than 15 of the sampled quadrats and

were, therefore, not considered in most analyses. Means, ranges, and especially CV values for five species (*C. disperma* Dewey, *C. exilis* Dewey, *C. heleonastes* L. f., *C. utriculata* Boott, and *E. angustifolium* Honck.) that were each found in at least 17, but fewer than 50, quadrats should be interpreted with care. Four species infrequently observed in Schefferville fens (*C. brunnescens* (Pers.) Poir., *C. capillaris* L., *C. diandra* Schrank, and *C. vesicaria* L.) were not encountered in any of the 1609 sampled quadrats.

The three environmental factors represented distinct gradients that were only weakly correlated, although statistically significant due to large sample size (distance/depth: $r^2 = 0.043$, $P < 0.01$; distance/pH: $r^2 = 0.115$, $P < 0.01$; depth/pH: $r^2 = 0.034$, $P < 0.01$). While a few of the smaller fens showed increasing depth with distance from edge, most fens were mosaics of hummocks, hollows, lawns, and irregular pools; some had elongated low ridges or strings with a mix of small shrubs, herbs, and sedges alternating with elongated pools or flarks dominated by sedges and *Menyanthes trifoliata* L. Although many of the fens had large pools with deep water (> 1 m deep), no quadrats were sampled in these areas because no sedges occurred there. Rooting position in relation to water table varied among the sampled quadrats from –65 cm (pools) to +55 cm (hummocks) with a mean of 4.9 cm, a median of 4 cm, and 50% of the quadrats found in a much narrower range between –1 cm and +11 cm (Table 1, Fig. 1A). The 1609 sampled quadrats also exhibited a wide range of pH values (2.9–8.3) with ~50% of the quadrats having values between pH 4 and pH 6 (Fig. 1B). Due to the elongated shape of many fens and the fact that both small and large fens were sampled, 75% of the quadrats were located less than 45 m from the nearest edge, although individual quadrats ranged up to 120 m from the closest edge in larger fens (Fig. 1C).

Most sedge species showed a very narrow range of tolerance for rooting position relative to water table and considerable overlap along the depth gradient (Table 1, Fig. 1A). Approximately 75% of the species had mean and median depths between 0 and +15 cm and, with the exception of *Carex saxatilis*, all species had mean and median depth between –5 cm and +20 cm (Table 1, Fig. 1A). However, most species had at least a few occurrences with rooting positions more than 20 cm above the water table. In contrast, few species could tolerate rooting positions more than 20 cm below the water table. Only *C. rostrata* Stokes and *C. utriculata* occupied these greater depths with any frequency. *Carex saxatilis* and *C. utriculata* had the lowest depth means and medians, while *C. trisperma* Dewey and *C. vaginata* Tausch had the highest mean and median depths (Table 1, Fig. 1A).

Carex livida (Wahlenb.) Willd. and *Eriophorum angustifolium* were the most depth-specialized species rooting at or below the water table, as indicated by low CV values for rooting position, while *Trichophorum alpinum* (L.) Pers. and *E. viridicarinatum* (Engelm.) Fernald had the lowest CV values among species rooting > 5 cm above the water table (Fig. 1A, Table 1). Conversely, *C. rostrata*, *C. utriculata*, *C. oligosperma* Michx., *C. limosa*, and *C. aquatilis* were generalists for rooting position, with higher CV values, broad non-outlier ranges, and with outliers both below the first quartile (deeper water) and above the third quartile (high above the water table) (Fig. 1A).

As a whole, sedge species in these fens showed a broader tolerance to the pH gradient than to the depth gradient and a steady and continuous separation along the pH gradient (Fig. 1B), with the range of pH means spanning from 3.96 for *Carex oligosperma* to 6.05 for *C. heleonastes* (Table 1). The highest pH values recorded were just above 8, with several species including *C. canescens* L., *C. gynocrates* Wormsk., and *C. aquatilis* having ranges that extended into these high pH regions. Although the ranges show potential overlap among all sampled sedges, four species (*C. oligosperma*, *C. trisperma*, *C. pauciflora* Lightf., and *C. magellanica* Lam.) had 75% of their occurrences in areas with pH values below 5.3 and means < pH 5), while four other species (*C. chordorrhiza* L. f., *C. heleonastes*, *C. leptalea* Wahlenb., and *Trichophorum alpinum*) had 75% of their occurrences in areas with pH values above 5.3 and means > pH 5.8 (Fig. 1B).

Species exhibiting the narrowest pH tolerances were *Carex heleonastes* and *Trichophorum alpinum* at the high end of the gradient (5.5–6.5); *C. exilis*, *C. disperma*, and *Eriophorum angustifolium* in the middle of the gradient (4.5–5.5); and *C. trisperma* and *E. vaginatum* at the low end of the gradient (3.5–4.5) (Table 1, Fig. 1B). With the exception of *T. alpinum*

Table 1. Means, standard deviations (SD), and coefficients of variation (CV) for rooting position in relation to water table (cm), water pH, and distance from the edge (m) for the 27 sedge species (Cyperaceae) in 21 fens in the Schefferville region of subarctic Quebec. Abbreviations used in Figures 1 and 3 and taxonomic sections for the *Carex* species are also included. Sample size refers to the number of quadrats in which the species was found out of 1609 quadrats.

				Rooting position (cm)			Water pH			Distance from edge (m)		
Species	**Abbreviation**	***Carex* Section**	**Sample size**	**Mean**	**SD**	**CV**	**Mean**	**SD**	**CV**	**Mean**	**SD**	**CV**
C. aquatilis Wahlenb.	Caqu	*Phacocystis* Dumort.	608	8.2	8.9	12.1	5.61	0.96	17.02	30.7	24.9	81.3
C. canescens L.	Ccan	*Glareosae* G. Don	57	9.0	10.5	14.2	5.57	1.17	20.95	34.9	26.5	76.0
C. chordorrhiza L. f.	Ccho	*Chordorrhizae* (Heuff.) Meinsh.	146	5.8	7.9	11.1	5.81	0.80	13.69	47.1	28.6	52.7
C. disperma Dewey	Cdis	*Dispermae* Ohwi	20	11.4	7.3	9.5	5.32	0.88	16.56	15.1	12.0	79.6
C. exilis Dewey	Cexi	*Stellulatae* Kunth	26	6.8	9.8	13.7	4.99	0.70	13.97	34.8	19.0	54.5
C. gynocrates Wormsk.	Cgyn	*Physoglochin* Neck. ex Dumort.	150	12.6	8.3	10.7	5.61	0.97	17.27	20.2	17.5	86.5
C. heleonastes L. f.	Chel	*Glareosae* G. Don	35	3.6	7.3	10.7	6.05	0.57	9.42	35.3	26.5	75.1
C. interior L. H. Bailey	Cint	*Stellulatae* Kunth	95	7.7	8.3	11.4	5.00	0.87	17.43	23.2	16.6	71.6
C. leptalea Wahlenb.	Clep	*Leptocephalae* L. H. Bailey	117	11.1	9.6	12.6	5.93	0.96	16.13	29.2	20.3	69.6
C. limosa L.	Clim	*Limosae* Tuck.	693	1.0	7.7	11.7	5.15	1.04	20.19	39.8	26.0	65.3
C. livida (Wahlenb.) Willd.	Cliv	*Paniceae* G. Don	226	−1.1	5.3	10.8	5.65	0.84	14.92	48.4	24.1	56.1
C. magellanica Lam.	Cmag	*Limosae* Tuck.	287	8.5	8.1	11.1	4.55	0.82	17.90	21.2	21.7	102.1
C. pauciflora Lightf.	Cpau	*Leucoglochin* Dumort.	188	12.4	7.7	10.0	4.32	0.57	13.13	23.1	19.4	84.0

C. oligosperma Michx.	Coli	*Vesicariae* (Heuff.) J. Carey	207	3.9	8.9	12.9	3.96	0.80	20.14	23.0	19.1	83.2
C. rariflora (Wahlenb.) Sm.	Crar	*Limosae* Tuck.	122	11.0	8.1	10.6	5.17	0.85	16.40	30.2	22.2	73.4
C. rostrata Stokes	Cros	*Vesicariae* (Heuff.) J. Carey	321	–1.1	12.8	20.1	5.02	0.81	16.11	39.0	28.5	73.1
C. saxatilis L.	Csax	*Vesicariae* (Heuff.) J. Carey	12	–11.6	26.0	48.6	5.90	0.83	14.03	16.3	6.4	39.3
C. tenuiflora Wahlenb.	Cten	*Glareosae* G. Don	51	11.6	11.4	14.9	4.90	0.89	18.25	25.1	22.2	88.5
C. trisperma Dewey	Ctri	*Glareosae* G. Don	85	16.2	10.9	13.4	4.14	0.60	14.38	10.6	10.4	97.8
C. utriculata Boott	Cutr	*Vesicariae* (Heuff.) J. Carey	17	–4.3	17.1	28.2	5.05	0.90	17.74	13.3	15.1	113.9
C. vaginata Tausch	Cvag	*Paniceae* G. Don	164	14.2	9.8	12.3	5.18	1.05	20.17	18.5	16.8	90.9
E. angustifolium Honck.	Eang	NA	41	0.5	6.3	9.6	4.82	0.46	9.57	10.8	8.7	80.5
E. chamissonis C. A. Mey.	Echa	NA	195	–0.3	7.2	11.1	4.77	0.83	17.40	36.4	27.4	75.5
E. vaginatum L.	Evag	NA	4	8.3	10.0	13.7	3.55	0.30	8.45	7.9	4.1	52.2
E. viridicarinatum (Engelm.) Fernald	Evir	NA	86	5.8	6.5	9.1	5.79	0.87	15.08	49.1	27.3	55.6
T. alpinum (L.) Pers.	Talp	NA	169	7.3	6.4	8.8	6.02	0.68	11.28	44.7	23.1	51.7
T. cespitosum (L.) Hartm.	Tces	NA	527	4.9	7.0	10.0	5.15	0.99	19.18	38.3	23.4	61.2
All quadrats			1609	4.9	11.4	16.3	5.00	1.05	20.94	30.5	25.1	82.3

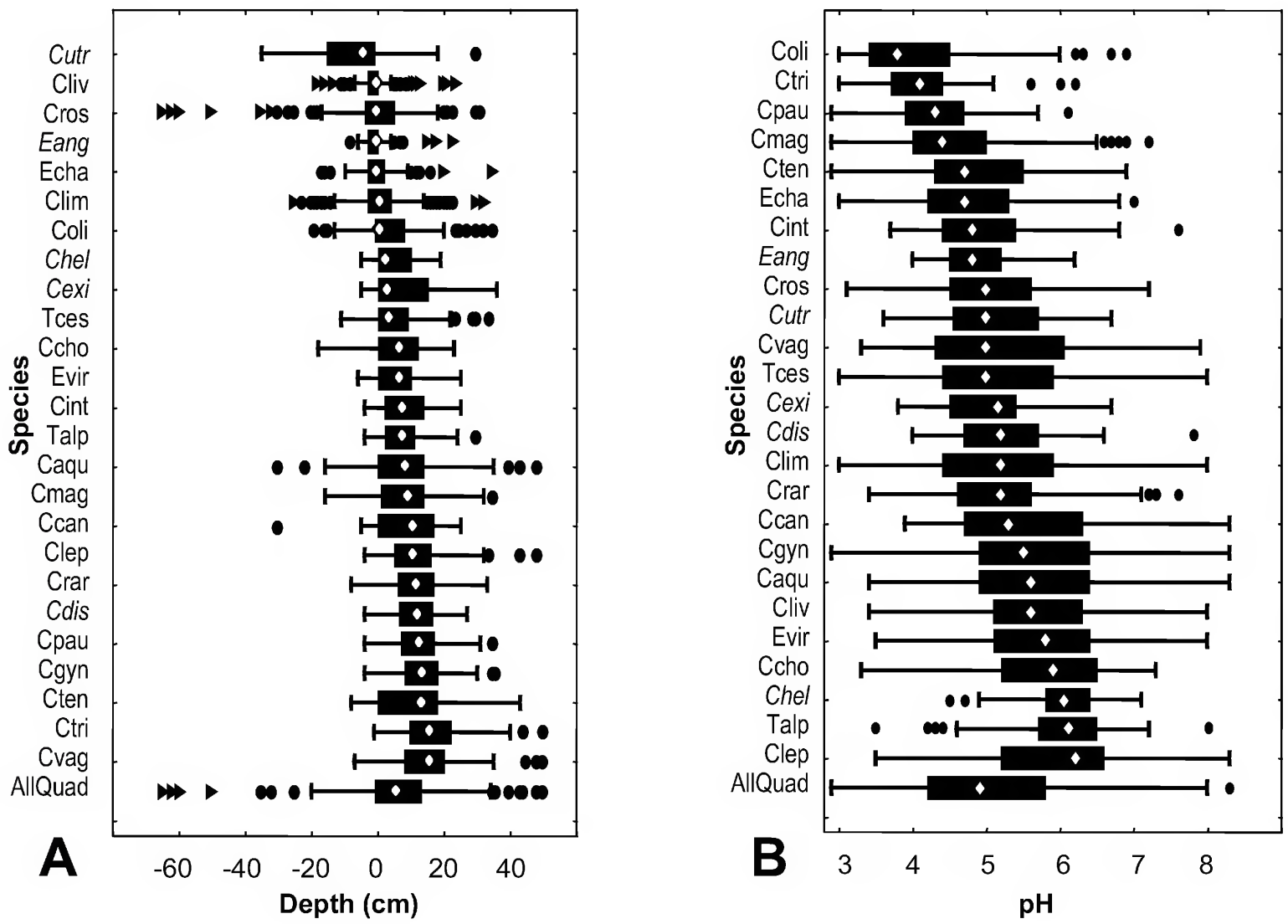

Figure 1. Box plots representing: (A) rooting position relative to water table (cm), (B) water pH, and (C) distance from nearest fen edge (m) for the 25 most common sedge species sampled in 21 fens of Schefferville region, northern Quebec. Species are arranged by increasing medians. The box represents values between the 25th and 75th percentiles while outliers and extreme outliers are defined as data values larger than the 75th percentile plus a coefficient multiplied by the width of the box, and data values smaller than the 25th percentile minus the coefficient multiplied by the width of the box. Coefficients are equal to 1.5 for outliers and 3 for extreme outliers. Full names for species are specified in Table 1. Abbreviations for species found in fewer than 50 quadrats are italicized.

and *C. trisperma*, all of these species occurred in fewer than 50 quadrats. The largest pH tolerances were shown by the species encountered most frequently: *C. limosa*, *C. aquatilis*, and *T. cespitosum* (Table 1). However, *C. gynocrates* and *C. leptalea*, both encountered in < 200 quadrats, also had high CV values and broad ranges on the pH gradient (Table 1, Fig. 1B).

All species except those found in only a few quadrats (e.g., *Carex saxatilis*) had high CV values and broad ranges on the distance gradient, and most had median values close to the overall median for all sampled quadrats (Table 1, Fig. 1C). Among those encountered in more than 50 quadrats, *C. trisperma* had the lowest mean and median distance from the nearest edge, while *C. chordorrhiza*, *C. livida*, *Trichophorum alpinum*, and *Eriophorum viridicarinatum* had the highest mean and median distances from the fen edge (Table 1, Fig. 1C). With the exception of *C. heleonastes*, *C. livida*, and *C. exilis*, all other species appeared at the edge of the fen (distance 0 m) at least once (Fig. 1C).

In contrast to the univariate box plots, the response surfaces (Fig. 2) and the CCA ordination (Fig. 3A) incorporate species abundance data from each quadrat and portray the distribution of species in relation to more than one gradient simultaneously. The negative exponential smoothing surface plots (Fig. 2) provide quick visual reference of the combinations of water pH and depth at which each species is expected to show highest abundance. On the CCA biplot (Fig. 3), lines representing the environmental factors are scaled to represent their relative influence on community structure and show that depth and pH are more important than distance. The orthogonal position of the depth and pH lines suggests that these two factors are independent, but distance has a weak negative correlation with depth (Fig. 3). Depth is most strongly correlated (r = 0.819) with the first axis (eigenvalue 0.329), while pH is most strongly correlated (r = 0.907) with the second axis (eigenvalue 0.256). Distance from the nearest fen edge has the highest correlation (r = 0.689) with the third axis (eigenvalue 0.048), but this axis represents very little of the variance in the data.

The points for each species represent the centroids of their distribution within the environmental space, such that species near each other are likely to occur in the same conditions (Fig. 3A). Widely spread distribution of the sampled quadrats across the ordination space (Fig. 3B) suggests highly heterogeneous microhabitats present across the 21 sampled fens. The relatively even spread of these points over the environmental space (Fig. 3A) suggests that these sedge species have differentiated to occupy different suites of environmental conditions, even though there is overlap among species on each of the environmental gradients (Fig. 1). Species are quite evenly spaced along the depth axis, but skewed toward higher values along the pH axis. Only three species (*Carex trisperma*, *C. pauciflora*, and *C. oligosperma*) occur most commonly at lower pH, and all three are clearly differentiated on the depth gradient (Fig. 3A). Based on 95% confidence ellipses plotted on the CCA quadrat ordination plot, *Carex* species belonging to the same section show substantial overlap. However, for many sections (e.g., *Paniceae* G. Don, *Glareosae* G. Don; Fig. 3C, D), the ellipses for closely related species differ in position, orientation, and shape.

Carex rostrata, *C. utriculata*, *C. livida*, *C. limosa*, *C. oligosperma*, and *Eriophorum chamissonis* C. A. Mey. are positioned on the right side of the CCA ordination plot, indicating rooting deeper below the water table, while *C. vaginata*, *C. gynocrates*, *C. leptalea*, *C. trisperma*, and *C. disperma* fall on the left side of the plot, suggesting preference for rooting higher above the water table. This is well illustrated by the negative exponential surface plots, which show the optimal abundance peaks in the regions of relatively deep water for *C. livida*, *C. rostrata*, *E. chamissonis*, and *C. limosa*, and optimal abundance peaks high above the water table for *C. leptalea*, *C. gynocrates*, and *C. vaginata* (Fig. 2). Both the surface plots and the CCA biplot suggest that not all species rooted in deeper water are likely to grow together: *C. oligosperma* usually occurs at low pH; *C. rostrata*, *C. utriculata*, *C. limosa*, and *E. chamissonis* at intermediate pH; and *C. livida* at high pH (Figs. 2, 3). Similarly, among the species rooting well above the water table, *C. trisperma* tends to grow at low pH; *C. vaginata* and *C. disperma* at intermediate pH; and *C. gynocrates* and *C. leptalea* at high pH (Figs. 2, 3).

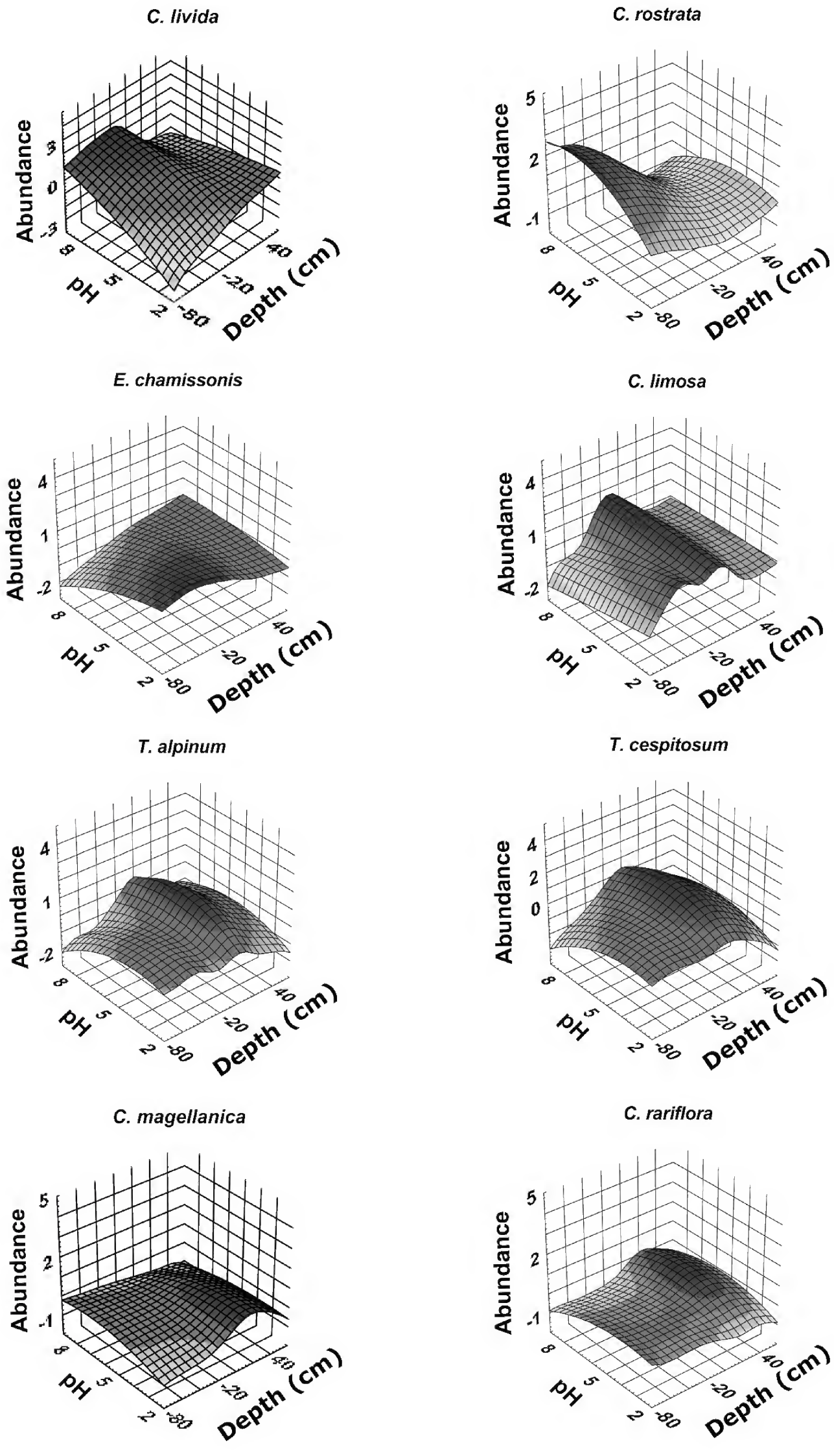

Figure 2. Negative exponential smoothing surface plots showing distribution and abundance along pH and depth gradients for species usually rooting below the water table in 21 fens of the Schefferville region, northern Quebec: *Carex livida*, *C. rostrata*, *Eriophorum chamissonis*, and *C. limosa*; species usually rooting near or just above the

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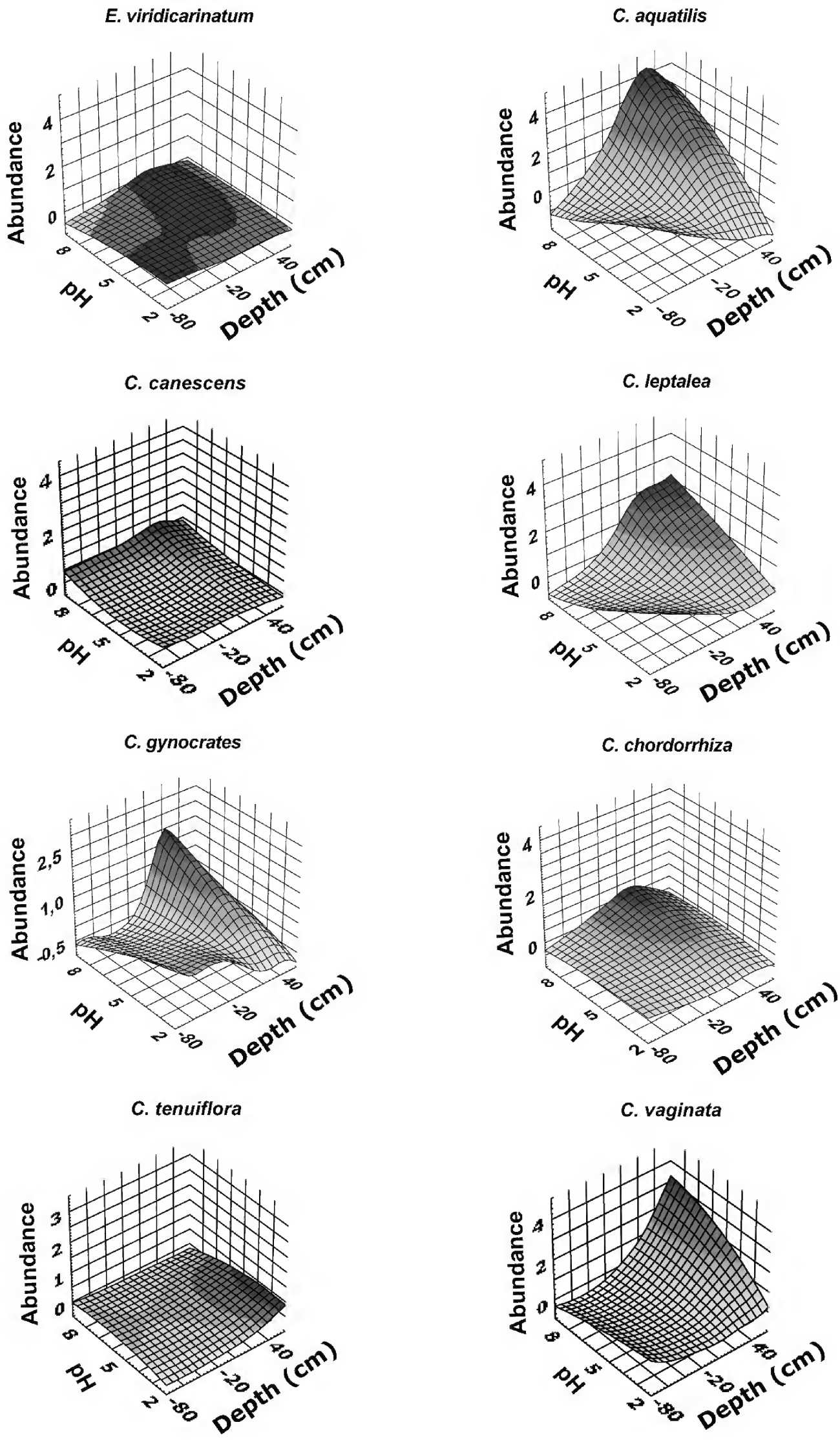

water table: *Trichophorum alpinum*, *T. cespitosum*, *C. magellanica*, *C. rariflora*, *E. viridicarinatum*, *C. aquatilis*, and *C. canescens*; and species most often rooting above the water table: *C. leptalea*, *C. gynocrates*, *C. chordorrhiza*, *C. tenuiflora* Wahlenb., and *C. vaginata*.

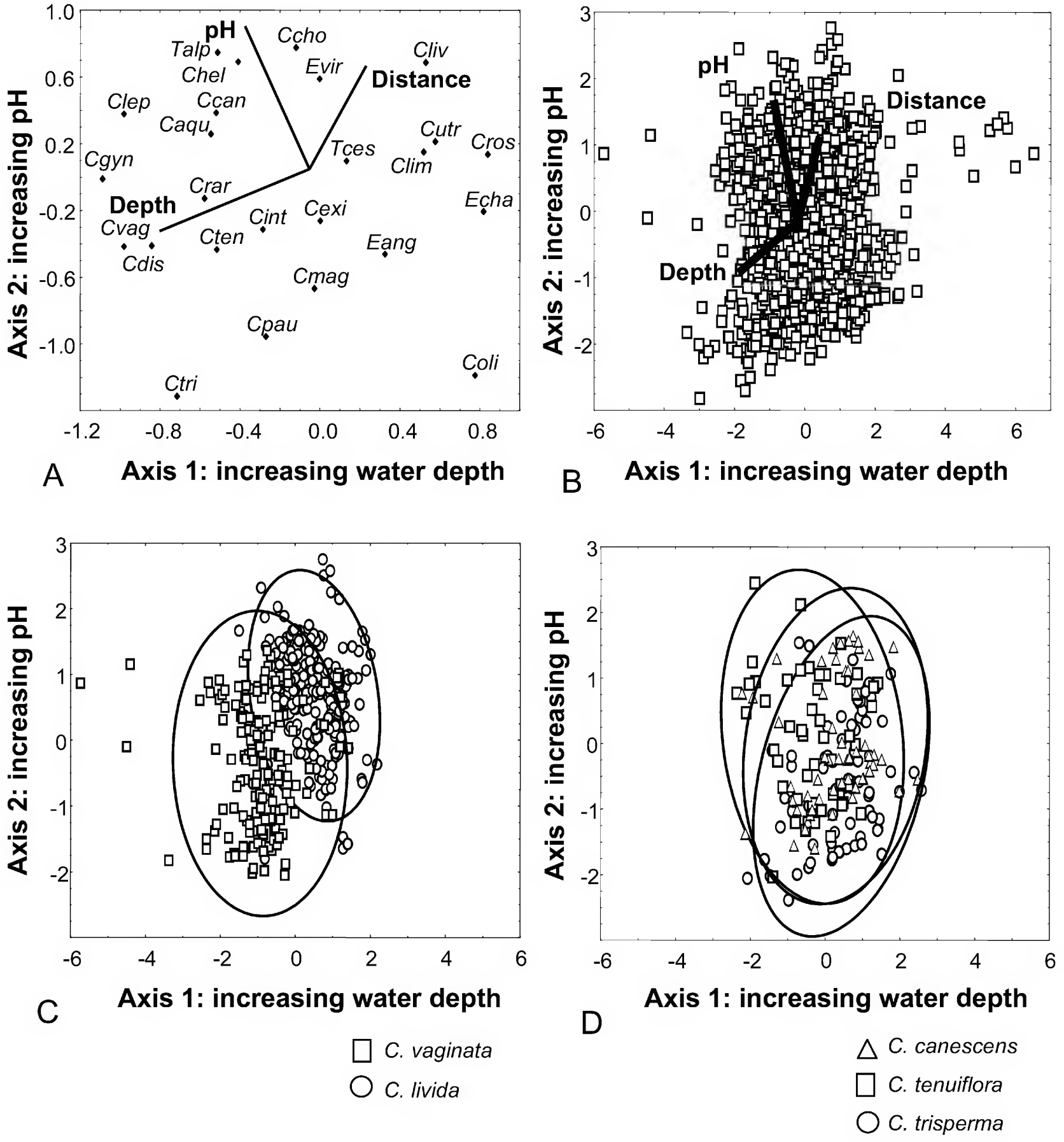

Figure 3. Canonical correspondence analysis (CCA) of (A) species, (B) quadrats, (C) quadrats, including 95% confidence region ellipses for *Carex livida* and *C. vaginata* (section *Paniceae*), and (D) quadrats, including 95% confidence region ellipses for *C. canescens*, *C. tenuiflora*, and *C. trisperma* (section *Glareosae*), performed on combined data from 21 Schefferville fens. Axes represent synthetic variables that are linear combinations of the three environmental factors. Rooting position relative to water table is most strongly correlated with the first axis (eigenvalue 0.329), pH with the second axis (eigenvalue 0.256), and distance with the third axis (eigenvalue 0.048). Axis 1 labeled "increasing water depth" indicates that the rooting position of the plants was found increasingly deeper below the water table. Full names of the species are specified in Table 1. For clarity, in parts C and D, only the quadrats where the species of interest was present are shown.

DISCUSSION

SEGREGATION ALONG ENVIRONMENTAL GRADIENTS

The sedge species examined in this study segregated along depth and pH gradients (Fig. 1) and showed preferences for different combinations of conditions when all three gradients were considered together (Figs. 2, 3). Rooting position relative to water table and water pH had the strongest influence on patterns of distribution, while distance from nearest edge had the least effect (Figs. 2, 3). Interestingly, the spread along the second axis of the CCA ordination, which is highly correlated with pH, is skewed toward higher pH values, suggesting that fewer of the sampled sedges are able to withstand acidic conditions.

Although most species root within a narrow range of water depth, these small differences in tolerance to submersion are important to community structure. Only species of large stature (e.g., *Carex rostrata* and *C. utriculata*) were able to tolerate rooting position more than 25 cm below the water table, but several relatively tall species (e.g., *C. aquatilis*, *C. oligosperma*, *Eriophorum angustifolium*, and *E. viridicarinatum*) were rarely or never found rooted below this depth, suggesting that rooting position is not simply a function of plant size. It is not surprising that the depth gradient has been identified as important in other peatland studies, since it affects aeration of the peat substrate, decomposition rates, solubility of mineral elements, and redox potential (Malmer, 1986; Bragazza & Gerdol, 2002), all of which can affect plant growth. Within heterogeneous fens, microhabitats differing in water depth often also differ in chemical composition and pH (Karlin & Bliss, 1984). In a recent review of gradient relationships in peatlands, Wheeler and Proctor (2000) stated that any categorization of mire vegetation based on water-table gradient is difficult due to local and temporal variation. In response to that, Økland et al. (2001) cited a number of studies in which the importance of water table to community composition and species abundance was clearly demonstrated, as was the case in this study.

While there has been general agreement on the importance of water pH and microtopography in structuring peatland communities, the nature and importance of the mire-margin to mire-expanse gradient have been more controversial (Wheeler & Proctor, 2000). Malmer (1986) considered this gradient to reflect important changes from the shallow, nutrient-rich margin to the deeper, nutrient-poor center of the peatlands. Økland et al. (2001) defended the importance of what they termed the swamp-forest to open-mire gradient (i.e., the distance from the fen margin), emphasizing differences in water-table fluctuations, aeration of peat, and shading along this gradient rather than pH or nutrient conditions. In our study, although the overall correlation across all fens between depth and distance from the nearest edge was very weak, we found that sedges most often encountered at fen edges (e.g., *Carex disperma*, *C. gynocrates*, *C. leptalea*, *C. pauciflora*, *C. trisperma*, and *C. vaginata*) were also among those rooted at the highest points above the water table, while sedges dominating deeper waters (e.g., *C. rostrata*, *C. utriculata*, *C. oligosperma*, *C. livida*, *C. limosa*, *C. saxatilis*, and *Eriophorum chamissonis*) were most abundant in open fen expanses. We also found a weak positive correlation between water pH and distance from nearest edge. However, sedges tolerant of low pH conditions (e.g., *C. pauciflora*, *C. trisperma*, and *C. magellanica*) were often found near some Schefferville fen margins, while species with a preference for higher pH (e.g., *C. gynocrates*, *C. leptalea*, *C. rariflora* (Wahlenb.) Sm., and *C. vaginata*) were commonly found near the margins of others. With the exception of *C. magellanica* and *C. rariflora*, these sedges that commonly grow along fen margins also grow in spruce-moss forests (Ball & Reznicek, 2002), suggesting that increased shading near the fen edge may contribute to differences in species composition along the margin-expanse gradient.

Minimal influence of the edge-to-center gradient on community structure in Schefferville fens (Fig. 3A) is probably a reflection of the heterogeneous topographic conditions within these fens. Sometimes the deepest pool of water was very close to the fen margin, with depth decreasing toward the fen center. A few fens had expanded margins with widely scattered small larch and spruce trees, while others had treed islands or ridges within open expanses of wet fen communities. The irregular distribution of hummocks, flarks, and pools in the fens of Schefferville, may, in essence, create an assemblage of miniature ecosystems, which may have differing depths and differing sources of mineral input (cf. Karlin & Bliss, 1984), making it difficult to detect clear trends along a gradient from edge to center.

SPECIALISTS AND GENERALISTS

Some sedges exhibited narrow tolerances on one or more of the three environmental gradients, while others showed broad tolerances along these gradients (Table 1, Fig. 1). Not surprisingly, some of the most common species (e.g., *Carex aquatilis*, *C. limosa*, and *Trichophorum cespitosum*) appeared to be generalists with respect to pH, while *C. aquatilis* was also a generalist with respect to rooting position relative to water table (Table 1, Fig. 1). In contrast, species like *C. livida* and *Eriophorum angustifolium* had very restricted distributions relative to the water table as well as fairly narrow distributions along the pH gradient (Table 1, Fig. 1), making them specialists. Some species that appear to be specialists in fens actually have broader distributions on the landscape. For example, *C. vaginata*, *C. gynocrates*, and *C. disperma* all had narrow tolerances along the depth gradient in this study (Figs. 1A, 2) but all can also be found in spruce-moss forests and along streams (pers. obs.), where they often root much higher above the water table than was possible in the fens we sampled.

The broad pH tolerance range for *Carex limosa*, the most common species in our study, has been reported elsewhere. For example, *C. limosa* was the dominant vascular plant in both rich and poor fens in western Alberta (Slack et al., 1980), a prominent plant of alkaline lake-edge communities in Michigan kettle-hole bogs (Vitt & Slack, 1975), and a species widely distributed across acidic and neutral conditions of mires in northern Japan (Yabe & Onimaru, 1997; Nakamura et al., 2002). Although relatively small (< 30 cm under subarctic conditions in the Schefferville region), *C. limosa* can root over a fairly broad range of water depths due to its extensive system of robust rhizomes.

Carex aquatilis, the second most frequent species in our sample, was also a generalist, although with some preference for pH above 5. Although the species is relatively large compared to other carices in fens and is physically capable of growing in deeper water, it was more frequently encountered in shallow water and on hummocks (Table 1, Figs. 1–3). Its prevalence in shallow water is consistent with previous reports of *C. aquatilis* in shallow water tracts in west-central Wyoming (Cooper & Andrus, 1994), on hummocks in Alberta peatlands (Karlin & Bliss, 1984), and in shallow fen pools and upslope margins of patterned fens in southeastern Labrador (Foster & King, 1984). It is difficult to conclude whether this species is more fit in shallow waters with its occasional presence in deeper water (especially outside of fens) simply due to chance establishment, or whether the species is a poor competitor excluded by other deep-water sedge species. In one small (0.25 ha.) fen, *C. aquatilis* dominated in shallow water but was almost completely replaced by *C. rostrata* in deeper water. *Carex aquatilis* may be an opportunist: a species with a wide range of tolerance for a diversity of environmental conditions, yet not a strong competitor, thus colonizing sites that are not suitable for other species in the local species pool.

Trichophorum cespitosum, with its short stature (< 30 cm) and densely tufted growth form, is the third widespread generalist found in this study. It has been reported as a dominant vascular plant of surfaces elevated 5–20 cm above the water table in patterned fens of southeastern Labrador (Foster & King, 1984). This species occurred most often on hummocks, giving it an abundance peak on the response surface at approximately 30 cm above the water table (Fig. 2); however, we also observed it on isolated hummocks totally surrounded by shallow water. *Trichophorum cespitosum* was also abundant across the pH range; however, its peak in abundance was reached at higher pH values (Fig. 2). Indeed, the species is generally considered an indicator of high pH and mineral conditions, and was reported as such in strongly minerotrophic peatlands of central Alberta (Karlin & Bliss, 1984), in rich spring-fen channels of northern Minnesota (Glaser et al., 1990), in high pH open low-shrub fens of mid-boreal Ontario (Bubier, 1995), and in moderately rich fens of Maine (Anderson et al., 1996).

Previous studies of peatland vegetation have identified suites of indicator species. For example, *Carex chordorrhiza*, *C. gynocrates*, *C. interior* L. H. Bailey, *C. leptalea*, *C. livida*, *C. rostrata*, *C. vaginata*, *Eriophorum viridicarinatum*, *Trichophorum alpinum*, and *T. cespitosum* were indicators for rich fen conditions in Alberta (Vitt et al., 1975; Slack et al., 1980; Karlin & Bliss, 1984), Minnesota (Glaser et al., 1990), Ontario and northern Quebec (Bubier, 1995), Maine (Anderson et al., 1996), and the Italian Alps (Bragazza & Gerdol, 2002). In Schefferville fens, eight of these species were almost always found at higher pH sites,

as expected; however, *C. interior*, *C. rostrata*, and *T. cespitosum* all occurred across a wider range of environmental conditions than expected for a rich fen indicator species. Among the high pH indicators, *C. chordorrhiza* and *C. livida* were usually found in wetter areas, while *C. gynocrates* and *C. leptalea* rooted in moss hummocks.

Indicator species for oligotrophic conditions (e.g., *Carex oligosperma*, *C. pauciflora*, and *C. trisperma*) have also been specified from the studies cited above or those in Labrador (Foster & King, 1984; Foster et al., 1988), Ontario (Vitt & Bayley, 1984), and Michigan (Vitt & Slack, 1975). Among these species, *C. oligosperma* grows in wetter areas, while *C. pauciflora* and *C. trisperma* grow on hummocks or fen margins. With the few exceptions noted above, these widespread, often circumboreal sedges have remarkably similar microhabitat preferences across their ranges. In this study, we sometimes detected broader tolerance ranges on one or more environmental gradients, but not dramatically different positions along them.

Some sedges we sampled in Schefferville fens are also found in habitats with different environmental conditions. For example, *Carex canescens*, *C. trisperma*, and *C. vaginata* are known to be abundant in moist, boreal spruce forests (Gleason & Cronquist, 1991; Johnson et al., 1995) while other species occur in moist alpine tundra, especially calciphiles, like *C. vaginata* and *C. rariflora* (Vellend & Waterway, 1999). For these species and for *C. leptalea*, which also grows in spruce-moss forests in Schefferville (pers. obs.), the response surface plots (Fig. 2) all show pronounced increases toward the extremes of both depth and pH gradients. This suggests that their optimal growing conditions may be found in places other than fens, especially where the substrate is drier and at higher pH. Similarly, the response surfaces for *C. rostrata* and *Eriophorum chamissonis* suggest optima in deeper water, a finding consistent with their occurrence on lakeshores and pond edges within the Schefferville region (pers. obs.).

RELATIONSHIPS AMONG CO-OCCURRING SPECIES

Species near each other on the CCA biplot (Fig. 3) are presumed to co-occur frequently because they have similar tolerances along the measured environmental gradients. For example, *Carex limosa*, *C. utriculata*, and *Trichophorum cespitosum* have very similar centroids for their distribution and frequently co-occur (Fig. 3). What prevents competitive exclusion? Based on the box plots and response surfaces, these three species probably avoid competition by rooting at different depths (*C. utriculata* deeper than *C. limosa*), or by having different growth forms (*C. limosa* with rhizomes and *T. cespitosum* in dense clumps), which may reflect different strategies for nutrient capture. *Carex limosa* was also very close on the depth gradient to *C. livida*, and the two species often co-occur, likely because *C. limosa* has a broad pH tolerance that subsumes the narrow tolerance zone of *C. livida*. The morphology of these two species also suggests a different strategy for nutrient capture: *C. limosa* has culms that eventually become prostrate and send up new shoots from the nodes, resulting in a very shallow tangle of rhizomes in a mud-bottom community, while *C. livida* has deeper, true rhizomes and sends roots much deeper into the peat substrate.

Carex aquatilis (rhizomatous) and *C. canescens* (caespitose) also frequently grow together in lawns or low hummocks and often colonize the edges of pools within patterned fens. In this case, there appears to be an interaction between the two species: seedlings of *C. canescens* are likely to establish on the peat captured by *C. aquatilis* rhizomes as they extend into pools and flarks. An example of coexistence in drier sites is that of *C. vaginata* and *C. disperma*, which grow together on hummocks, as was observed in our study, and are also reported from wooded peatlands of Maine (Anderson et al., 1996). *Carex vaginata* is a more robust species that roots deeper than the smaller delicate plants of *C. disperma*. Further study of the physiological basis for these patterns of co-occurrence is needed.

One consistent and noteworthy observation from the CCA plot is that species with similar preferences on these environmental gradients tend to belong to different sections of *Carex* or different genera within Cyperaceae. On the other hand, closely related species, such as the three representatives of section *Limosae* Tuck., segregate along the gradients. Whereas *C. limosa* and *C. magellanica* occupy quite different positions on the depth gradient, *C. rariflora* segregates from both species along the pH gradient (Fig. 3A). The 95% confidence region ellipses for these three species differ in position,

size, and shape, despite considerable overlap. Furthermore, rooting positions relative to water table differed significantly for *C. limosa* (mean = –1.7 cm) and *C. magellanica* (mean = +4.7 cm) in a more targeted study where rooting positions were measured immediately adjacent to each species, rather than in the center of a sampling quadrat (Dabros & Waterway, 2004). Similarly, *Eriophorum angustifolium* and *E. viridicarinatum* occupy nearly identical positions on the depth gradient, but clearly segregate along the pH gradient, as do three species in *Carex* section *Glareosae* (Fig. 3A, D). In contrast, *C. livida* and *C. vaginata* (section *Paniceae*) clearly segregate on the depth gradient but have similar tolerances on the pH gradient (Fig. 3A, C). These observations are consistent with the hypothesis that niche differentiation among closely related species plays a role in fen community structure and may contribute to the high diversity of Cyperaceae found in these habitats. However, further investigation of the physiological basis for differentiation along the environmental gradients and significance testing of the relationship between ecological distance and phylogenetic distance are needed.

Acknowledgments

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Chapter 7

The *Carex* Flora of Quebec – Labrador North of 54°N

Jacques Cayouette

ABSTRACT The *Carex* L. flora of Quebec-Labrador north of lat. 54°N was surveyed as part of a joint floristic project headed by Laval University, Quebec, Canada. The sedge family (Cyperaceae) is the largest family of vascular plants in the study area, dominant both in local floras (15%–20% of taxa) and in the area as a whole (16%), with eight genera and 123 taxa. *Carex* is the largest genus with 97 taxa, with sections *Phacocystis* Dumort., *Glareosae* G. Don, *Vesicariae* (Heuff.) J. Carey, and *Racemosae* G. Don predominating. *Carex* species are found in all five recognized vegetation subzones ranging from coniferous forest to arctic herb tundra-subzones whose climatic and geologic history have produced a diversity of wetlands favored by these species. Boreal taxa are dominant (57%), followed by arctic (36%) and temperate (7%) taxa. In terms of their worldwide range, circumhemispheric taxa are dominant (54%), followed by North American (37%) and amphi-Atlantic taxa (9%). Rare taxa represent 23%, while 69% are moderately common, and 8% are very common and widespread. *Carex bigelowii* Torr. ex Schwein. is the most common species. Others are rare for various reasons: some reach their northern limit in the study area; some are confined to rare habitats; some may appear rare but are simply under-collected; and for some, the reasons for their limited range are unclear. High habitat diversity is related to the variety and extent of wetlands and peatlands, coupled with severe climatic conditions. Taxonomic problems exist in 46% of the taxa, and major taxonomic problems exist in pairs of closely related species, such as *C. heleonastes* L. f.–*C. marina* Dewey, *C. adelostoma* V. I. Krecz.–*C. buxbaumii* Wahlenb., *C. atrata* L.–*C. atratiformis* Britton, *C. media* R. Br. ex Richardson–*C. norvegica* Retz., *C. capillaris* L.–*C. krausei* Boeckeler, *C. membranacea* Hook.–*C. rotundata* Wahlenb., *C. rostrata* Stokes–*C. utriculata* Boott, *C. arctogena* Harry Sm.–*C. capitata* L., and *C. canescens* L.–*C. lapponica* O. Lang. Natural hybridization is important (18 recognized taxa), sometimes resulting in stabilized species of hybrid origin such as *C. recta* Boott, *C. salina* Wahlenb., and *C.* ×*flavicans* (F. Nyl.) F. Nyl. (*aquatilis* × *subspathacea*), a sedge that is becoming more widespread.

KEY WORDS *Carex*, Cyperaceae, floristics, phytogeography, Quebec-Labrador, rare taxa, systematics, wetlands.

The Cyperaceae is the most important family of vascular plants at northern latitudes, not only in terms of number of species (Ball, 1990), but also in plant cover, especially in wetlands. Sedges represent about 10% of Canada's floristic diversity (Catling et al., 1990). On the Quebec-Labrador Peninsula, the relative importance of the Cyperaceae increases with latitude. For example, at the northern limit of the temperate zone in Lévis County, Quebec, the sedge family makes up about 10% of recorded species (95 out of 937 species, Doyon & Cayouette, 1978). Farther north, in the boreal zone of eastern Quebec, the percentage of sedge species in the flora increases to 13% in Temiscouata County (100 out of 745, Lavoie, 1984a) and to 15% on the North Shore of the Gulf of St. Lawrence (56 out of 373, Lavoie, 1984b).

In both the arctic and boreal zones of Quebec-Labrador, north of 54°N, the proportion of Cyperaceae is higher and ranges from 15% to even 20% of the total flora: Salluit (arctic, 15%, Blondeau & Cayouette, 2002), Baie Wakeham and Havre Douglas (arctic, 16%, Blondeau & Cayouette, 2002), Kuujjuak (boreal, 17%, Blondeau & Cayouette, 2002), and Lac Chavigny (boreal, 20%, Cayouette, 1987). These proportions remain about the same when coastal and inland floras at the same latitudes are compared, even though coastal floras are much richer in species: coastal Golfe de Richmond (17% of 410 species, Payette & Lepage, 1977; Blondeau, 1986), inland Lac à l'Eau-Claire (16% of 250 species, Deshaye & Morisset, 1985).

The goal of this paper is to provide the first detailed analysis of the diversity of *Carex* L. in Quebec-Labrador north of 54°N in terms of taxonomy, phytogeography, abundance, and habitat diversity.

Material and Methods

THE STUDY AREA

Northern Quebec-Labrador is shown in Figure 1. This study of *Carex* of this region is part of an ongoing collaborative preparation of a flora of vascular plants found north of 54°N, spearheaded by Le Centre d'Études nordiques, Laval University, Quebec City, Canada. One of the reasons for selecting 54°N is that it marks, in this region, the southern limit of the arctic zone that runs down the coast of Hudson Bay to northern James Bay (Payette & Bouchard, 2001). The study area also includes adjacent islands in Hudson Bay (e.g., Belcher Islands) and Ungava Bay (e.g., Akpatok Island), which belong administratively to Canada's Nunavut Territory. The area covered by the projected flora is about half of the entire Quebec-Labrador Peninsula.

Two major vegetation zones are represented in the study area, the boreal and the arctic, which are in turn subdivided into three boreal and two arctic subzones (Fig. 1) (Payette & Bouchard, 2001). *Closed-crown forest* is very limited in the southeastern part of the boreal zone under consideration, whereas *lichen woodland* and *forest tundra* are more widespread. Lichen woodland consists of open coniferous forest characteristically dominated by black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) with carpets of lichens in the openings. In the forest tundra subzone, conifers are usually restricted to protected sites with treeless exposed areas of shrub tundra. This situation prevails northward up to the latitudinal tree line. In the southern part of the arctic zone, *shrub tundra* dominates, with low shrubs, mostly *Betula glandulosa* Michx., ericaceous species, and lichens. The northern fringe of the Quebec-Labrador Peninsula is *herb tundra* subzone where grasses and sedges replace low shrubs.

SOURCES OF INFORMATION ON *CAREX*

The list of *Carex* species (Appendix 1) is based on two major sources: a preliminary report of the flora of northern Quebec-Labrador (Lavoie et al., 1987) and a survey of herbarium specimens from CAN, DAO, MT, MTMG, QFA, QFBE, QUE, and SFS (herbarium acronyms after Holmgren et al., 1990). That survey of more than 12,000 *Carex* specimens was databased for the project "Flore du Québec-Labrador nordique" of Centre d'Études nordiques and Herbier Louis-Marie (QFA), both of Laval University, Quebec. Species abundance was assessed from these sources.

Data on phytogeography are derived mainly from Hultén (1968) and Hultén and Fries (1986). Additional information is taken from Moore and Chater (1971), Porsild and Cody (1980), Reznicek and Ball (1980), Crins and Ball (1989), Ball (1990), Waterway (1994), Ball (2002a), Murray (2002a), Reznicek and Ford (2002), and Toivonen (2002).

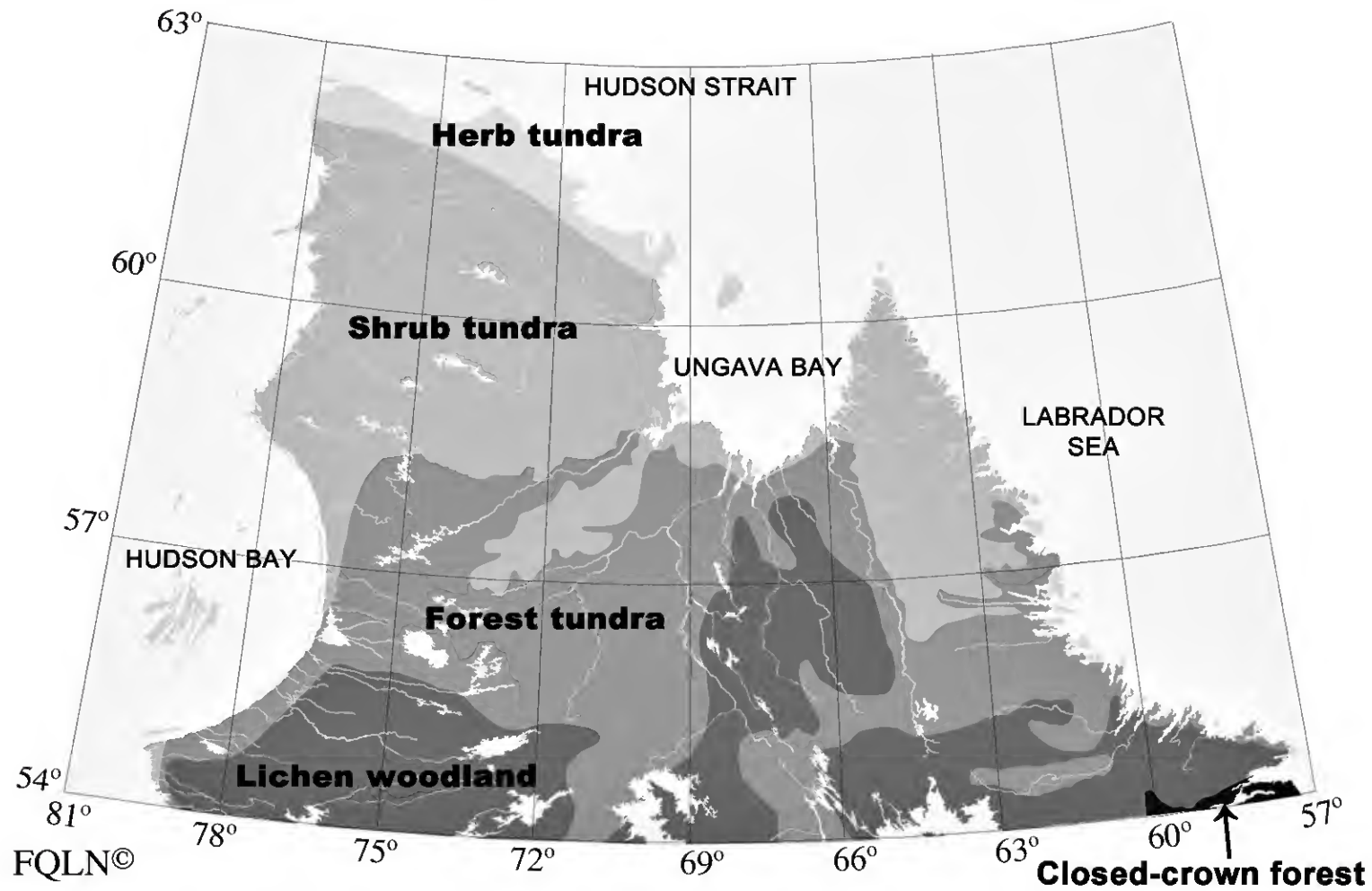


Figure 1. Map of Quebec-Labrador north of 54°N with the vegetation subzones (the lowest three are in the boreal zone, the upper two in the arctic). Used with permission of the Northern Québec-Labrador Flora project.

Information on the study area itself was also considered (Payette & Lepage, 1977; Deshaye, 1983; Morisset et al., 1983; Deshaye & Morisset, 1985; Blondeau, 1986, 1989a, b, 1990; Cayouette, 1987; Deshaye & Cayouette, 1988; Blondeau & Cayouette, 2002). Habitat diversity has been drawn from our own field experience, from the herbarium survey, and from the above list of references plus Dutilly and Lepage (1962, 1964) and Garneau (2001).

In general, the taxonomic treatments follow Volume 23 of *Flora of North America* (FNA), which treated the Cyperaceae. Sectional names are in accordance with the FNA treatments and Reznicek (2001). Authors for taxon names are provided in Appendix 1. Commentary on hybridization is based primarily on Cayouette (1990), Cayouette and Catling (1992), and Ford et al. (1993).

New data on *Carex lapponica* O. Lang and *C.* ×*flavicans* (F. Nyl.) F. Nyl. are based on examination of specimens borrowed from the above-mentioned herbaria as well as from BM and LKHD. Leaf width and perigynium measurements were taken from 10 specimens of both *C. canescens* L. subsp. *canescens* and subsp. *disjuncta* (Fernald) Toivonen from eastern North America, and from nine specimens of *C. lapponica* originating in Manitoba and Quebec (five measurements of each character in the plot diagram; see Fig. 4G).

Results and Discussion

Number of Species and Sections

Sedges are well represented in every subzone north of 54°N. Together with the Poaceae, they dominate the local flora. A preliminary survey of the flora of the project area has revealed a total of 755 taxa. The Cyperaceae dominate with 123 taxa (16% of the flora) followed by the Poaceae with 86 (11%). The 123 taxa of Cyperaceae, including 97 species and various hybrids, can be assigned to eight genera: *Blysmopsis* Oteng-Yeb. (1), *Eleocharis* R. Br. (5), *Eriophorum* L. (14), *Kobresia* Willd. (2), *Rhynchospora* Vahl (1), *Scirpus* L. (1), *Trichophorum* Pers. (2), and *Carex* (97).

A preliminary list of *Carex* in Quebec-Labrador north of 54°N is given in Appendix 1. There are 78 species, three with two subspecies, and 16 hybrids,

Table 1. Phytogeographical elements, abundance, habitats, and taxonomic problems of the *Carex* flora of Quebec-Labrador north of 54°N.

Elements	No.	%
A) PHYTOGEOGRAPHY		
1) Phytogeographical groups		
Arctic (a)	13	16
(Low Arctic) (la)	1	1
Arctic-alpine (aa)	15	19
ARCTIC TOTAL	29	36
(High Boreal) (hb)	1	1
Boreal (b)	45	56
BOREAL TOTAL	46	57
TEMPERATE TOTAL	6	7
Bipolar (*)	6	7
2) Geographical elements		
Circumpolar (cp)	15	19
Circumpolar disjunct (cpd)	6	7
Circumpolar s.l.	21	26
Circumboreal (cb)	16	20
Circumboreal disjunct (cbd)	7	9
Circumboreal s.l.	23	28
Circumhemispheric	44	54
Amphi-Atlantic (amp)	7	9
Cordilleran (co)	2	2
North American (na)	15	18
North American + East Asian (na-ea)	5	6
Northeastern American (nea)	7	9
Northeastern American + East Asian (nea-ea)	1	1
North American s.l. (incl. Cordilleran)	30	37
B) ABUNDANCE		
Rare, 12 or fewer sites (1)	19	23
Moderately common (2)	56	69
Very common and widespread (3)	6	8
C) HABITATS		
Wetlands, including peatlands and salt marshes (w)	46	58
Shores (of rivers, brooks, ponds, lakes) (s)	42	52
Wetlands or shores	63	77
Mesic (m)	17	21
Dry (d)	13	16
Mud boils (mb)	6	8
Snow beds (sb)	12	15
Coastal (c)	10	12
Obligate calcicolous (ca)	5	6
D) TAXONOMIC PROBLEMS		
Species complex (sc)	18	22
Infraspecific variation (iv)	4	5
Hybrids (h) [based on 97 taxa]	18	19
Total number of taxa considered	81	100

Table 2. Recent status of the six bipolar *Carex* species reported for northern Quebec-Labrador.

Taxa (sensu lato)	Northern Hemisphere	Southern Hemisphere	References
canescens	*curta* Gooden. [var. *curta*]	*curta* var. *robustior* (Blytt ex Andersson) D. M. Moore & Chater	Moore & Chater, 1971
	canescens	*canescens*	Ball, 1990
	subsp. *canescens*		Toivonen, 2002
	subsp. *disjuncta* var. *robustior* Blytt ex Andersson (?)	var. *robustior* (?)	Toivonen, 2002
capitata	*arctogena*	*arctogena* (?)	Smith, 1940
	capitata		Smith, 1940
	—	*antarctogena* Roiv.	Roivainen, 1954
	capitata var. *capitata*	*capitata* var. *arctogena* (Harry Sm.) Hultén	Moore & Chater, 1971
	capitata	*arctogena*	Reinhammar & Bele, 2001
	arctogena		Reinhammar & Bele, 2001
	capitata	*capitata*	Murray, 2002b
macloviana	*macloviana*	*macloviana*	Moore & Chater, 1971; Whitkus & Packer, 1984; Mastrogiuseppe et al., 2002
magellanica	subsp. *irrigua*	subsp. *magellanica*	Moore & Chater, 1971; Ball, 2002b
	paupercula	*magellanica*	R. Elven, pers. comm.
maritima	*maritima*	*maritima*	Moore & Chater, 1971; Reznicek, 2002
microglochin	—	*microglochin*	Roivainen, 1954
	—	"*oligantha* (Boott) Kük."	Roivainen, 1954
	subsp. *microglochin*	subsp. *fuegina* Kük.	Moore & Chater, 1971; Cochrane, 2002

for a total of 97 taxa. They belong to 33 sections of which 19 are monotypic. The largest sections in the flora are *Phacocystis* Dumort. (16 taxa including hybrids), *Glareosae* G. Don (15), *Vesicariae* (Heuff.) J. Carey (10), and *Racemosae* G. Don (9).

Ball and Mastrogiuseppe (2002) considered *Carex atrofusca* Schkuhr to be part of section *Aulocystis* Dumort., together with *C. fuliginosa* Schkuhr and *C. petricosa* Dewey var. *misandroides* (Fernald) B. Boivin. However, Egorova (1999) includes *C. atrofusca* in section *Chartoteuchium* (Börner) V. I. Krecz., a section not recognized by North American caricologists. *Carex atrofusca* differs from the other *Aulocystis* in having very flat and papillate perigynia with mostly smooth margins toward the apex and long stipitate achenes that are very small compared to the perigynia. These differences warrant placing *C. atrofusca* in section *Chartoteuchium*.

PHYTOGEOGRAPHY

For purposes of this study, phytogeographical characteristics have been classified on the basis of two sets of considerations, as detailed in Table 1. One set relies on bioclimatic data and vegetation zones that tend to vary with latitude. The other one, in contrast, corresponds to the world range of plants and is given according to the longitudes. For the 81 species and subspecies of *Carex* found in northern Quebec-Labrador, this information is provided in Appendix 1 and summarized in Table 1. The 16 hybrid taxa are excluded from Table 1.

According to their affinities to vegetation zones, boreal taxa dominate (57%), followed by arctic (36%) and temperate elements (7%) (Table 1). Arctic-alpine taxa comprise 19% of the total. Only one low arctic (*Carex adelostoma* V. I. Krecz.) and one high boreal species (*C. lapponica*) have been identified. Thus few species are restricted to these subzones.

There are six taxa that are called bipolar by, among others, Moore and Chater (1971) and Ball (1990): *Carex canescens* s.l., *C. capitata* L. s.l., *C. macloviana* d'Urv., *C. magellanica* Lam. s.l., *C. maritima* Gunnerus, and *C. microglochin* Wahlenb. s.l. (Table 1). Although Moore and Chater (1971) claimed that they observed few differences between individuals originating in different hemispheres, only a very few recent studies have reconsidered the situation. This information is summarized in Table 2. As far as *Carex magellanica* is concerned, the typical subspecies is considered to be limited to the Southern Hemisphere, with the northern taxon being called subspecies *irrigua* (Wahlenb.) Hiitonen. Some authors argue that the two subspecies of *C. magellanica* exhibit more differences than expected, and that they might reasonably be considered at the specific level (R. Elven, pers. comm.). Understood in this way, the northern taxon would be called *C. paupercula* Michx.

Within the study area, both boreal and arctic taxa may be considered in two categories: (1) boreal taxa and arctic taxa restricted to their respective zones, and (2) boreal taxa and arctic taxa that extend into each other's zone. Relatively common species belonging to these categories are listed in Table 3. There are nine entirely arctic taxa and 29 entirely boreal taxa. On the other hand, 17 arctic taxa extend into the boreal zone, and eight boreal taxa extend into the arctic zone. Most of the arctic element that extends into the boreal zone is also arctic-alpine.

The world range of the *Carex* taxa is divided in three large categories. Circumhemispheric taxa are the most numerous (54%), followed by North American (37%) and amphi-Atlantic taxa (9%) (Table 1). The first category usually is split up into phytogeographical affinities: circumpolar or circumarctic (26%) and circumboreal (28%). Circumpolar and circumboreal categories could also be divided according to the presence or absence of gaps in their respective ranges: there are a few more disjunct taxa (9%) in the circumboreal category than in the circumpolar one (7%) (Table 1). There are many categories within the North American group: sensu stricto (18%), North American and East Asian (6%), northeastern American (9%), and only one (1%) northeastern American and East Asian (*C. michauxiana* Boeckeler). *Carex macloviana* and *C. stylosa* C. A. Mey., two Cordilleran taxa (2%), are included in the North American group; as reported above, *C. macloviana* is also a bipolar species.

North of the study area, in the Canadian Arctic Archipelago, there is only one additional taxon, *Carex aquatilis* Wahlenb. var. *minor* Boott, also called *C. aquatilis* subsp. *stans* (Drejer) Hultén (Aiken et al., 1999). The observations recorded here indicate that in northern Quebec-Labrador, there are substantial numbers of species of *Carex* in both the

Table 3. Selection of relatively common *Carex* taxa considered arctic or boreal in Quebec-Labrador north of 54°N or extending also into an adjacent zone.

Arctic		Boreal	
Not extending into the boreal zone	Extending into the boreal zone	Not extending into the arctic zone	Extending into the arctic zone
C. atrofusca	*C. bicolor*	*C. arcta*	*C. aquatilis* var. *aquatilis*
C. fuliginosa	*C. bigelowii* subsp. *bigelowii*	*C. atratiformis*	*C. brunnescens* s.l.
C. holostoma	*C. capillaris*	*C. aurea*	*C. canescens* subsp. *canescens*
C. macloviana	*C. capitata*	*C. buxbaumii*	*C. chordorrhiza*
C. marina	*C. glacialis*	*C. deflexa* var. *deflexa*	*C. gynocrates*
C. membranacea	*C. glareosa* subsp. *glareosa*	*C. diandra*	*C. mackenziei*
C. rotundata	*C. lachenalii*	*C. disperma*	*C. tenuiflora*
C. ursina	*C. maritima*	*C. echinata* subsp. *echinata*	*C. vaginata*
C. williamsii	*C. microglochin*	*C. exilis*	
	C. nardina	*C. foenea*	
	C. norvegica subsp. *norvegica*	*C. garberi*	
	C. rariflora	*C. heleonastes*	
	C. rupestris	*C. lenticularis* var. *lenticularis*	
	C. saxatilis	*C. leptalea* subsp. *leptalea*	
	C. scirpoidea subsp. *scirpoidea*	*C. limosa*	
	C. subspathacea	*C. livida*	
	C. supina subsp. *spaniocarpa*	*C. magellanica* subsp. *irrigua*	
		C. norvegica subsp. *inferalpina*	
		C. oligosperma	
		C. paleacea	
		C. pauciflora	
		C. praticola	
		C. rostrata	
		C. salina	
		C. stylosa	
		C. trisperma	
		C. utriculata	
		C. vesicaria	
		C. viridula subsp. *viridula* var. *viridula*	

arctic and boreal zones, but it is in the boreal zone that the greatest number of species are found.

FREQUENCY

Three categories have been defined to characterize the frequency of *Carex* taxa in the study area (Appendix 1; Table 1). Six species (8%) are very common and widespread (level 3) in most of the vegetation subzones, both in the arctic and boreal zones: *Carex bigelowii* Torr. ex Schwein. (Fig. 2A), *C. capillaris* L., *C. norvegica* Retz. subsp. *norvegica*, *C. rariflora* (Wahlenb.) Sm., *C. saxatilis* L., and *C. scirpoidea* Michx. subsp. *scirpoidea* (see also Morisset et al., 1983). The majority (56: 69%) of the taxa (species including subspecies and varieties) are moderately common (level 2). At the other end of the scale, 19 taxa (23%) are rare or have a somewhat restricted range (level 1). They have been found in one to 12 sites each in the study area. The reasons for this can be explained in two categories: (1) species at their northern limit, (2) narrow ecological preferences.

Species at their northern limit

Fourteen rare temperate or boreal taxa reach the northeasternmost limit of their range in the Quebec-

Labrador Peninsula: *Carex adusta* Boott, *C. canescens* subsp. *disjuncta*, *C. castanea* Wahlenb. (Fig. 2B), *C. concinna* R. Br., *C. conoidea* Willd., *C. crawfordii* Fernald, *C. eburnea* Boott, *C. garberi* Fernald, *C. interior* L. H. Bailey, *C. leptonervia* (Fernald) Fernald, *C. michauxiana*, *C. pallescens* L., *C. petricosa* var. *misandroides*, and *C. recta* Boott. Most of these species are found in the southern parts of the study area or in geographically restricted sites along maritime coasts or rivers.

Narrow ecological preferences

Taxa that require rare substrates naturally tend to be rare. In the boreal zone, limestone and dolomite outcrops are rare, which leads to a restricted occurrence of the following obligate calcicolous taxa: *Carex castanea*, *C. concinna*, *C. eburnea*, and *C. petricosa* var. *misandroides*.

Two species, *Carex adelostoma* (collected at 12 sites) and *C. lapponica* (collected at three sites; Fig. 4A), are limited to a narrow strip either at the northern part of the boreal zone or at the southern limit of the arctic zone. The reasons for their scarcity are not understood. *Carex lapponica* does not seem to require a particular substrate. Its distribution could be the consequence of narrow ecological preferences or the result of a late postglacial migration (Cayouette, 1987). A few other vascular plant species show a similar pattern, such as the coastal *Castilleja raupii* Pennell and *Pedicularis sudetica* Willd., and also *Pinguicula villosa* L. and *Potentilla multifida* L. (Cayouette, 1986a).

HABITAT DIVERSITY

The reasons for the dominance of Cyperaceae in northern Quebec-Labrador are numerous but mostly related to the presence of large peatlands and water bodies. Historic and recent glacial events have favored permafrost conditions, varying from continuous to discontinuous, and this topic is extensively discussed by Payette (2001a). Superficial thawing processes during summer on the flat landscapes produce wet conditions that facilitate the development and spread of many sedge species. Sedges dominate both in terms of species numbers and frequency of occurrence in wet areas.

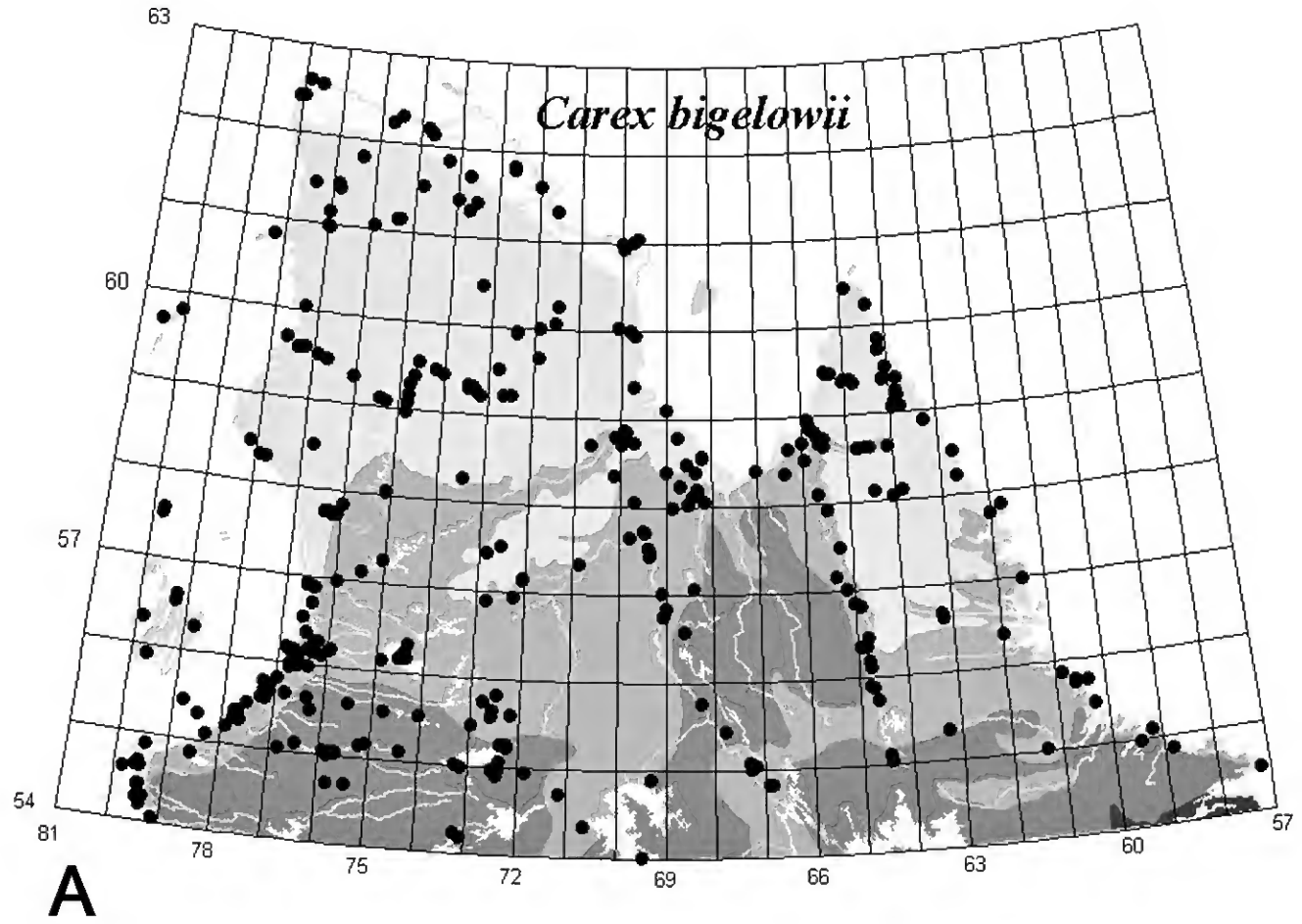
Most of the arctic and boreal environments have been described elsewhere (Rousseau, 1968; Payette, 2001b). However, in such a vast area, it has not been possible to report all habitats and their corresponding *Carex* flora. The major units and a few specialized habitats are reported here. In the following examples, the *Carex* species are not always unique to the habitat given, but might also be found in several environments. The information is provided in Appendix 1, summarized in Table 1, and briefly analyzed at the end of this section. Habitats for the hybrids also are provided in Appendix 1 and Table 1.

Coastal habitats are varied and rich. Their floras have more vascular plant species than inland floras at similar latitudes, a fact reflected by the number of *Carex* species. *Carex* richness may be due to earlier deglaciation along the coast. Specialized habitats such as salt marshes, a variety of dry, mesic, and wet rocky, gravelly, and sandy habitats, and diversified bedrocks, most of which are more common along the coast than inland, may also contribute to species richness (Morisset et al., 1983).

Ten species (12%) are considered to be restricted to the coast. Species found on mesic or dry rocky, gravelly, and sandy seashores are *Carex glareosa* Wahlenb. subsp. *glareosa*, *C. krausei* Boeckeler, *C. maritima*, and *C. praticola* Rydb. Wet coastal habitats include various salt marshes (Fig. 3A) and lagoons. The *Carex* species restricted to these habitats are *C. glareosa* subsp. *glareosa*, *C. mackenziei* V. I. Krecz., *C. paleacea* Schreb. ex Wahlenb., *C. recta*, *C. salina* Wahlenb., *C. subspathacea* Wormsk., and *C. ursina* Dewey. Almost all hybrids involving species of section *Phacocystis* are coastal.

Wetland communities are very frequent inland both in arctic and boreal zones. Shrub tundra and herb tundra are affected by continuous permafrost conditions. During the short summer, thawing occurs only in the active soil layer. This is the favorite habitat for *Carex atrofusca*, *C. bigelowii* subsp. *bigelowii*, *C. fuliginosa*, *C. holostoma* Drejer, *C. membranacea* Hook., *C. rariflora*, and *C. rotundata* Wahlenb.

Peatlands are widespread in all of the subzones and are dominated by minerotrophic peatlands (Payette, 2001b). Rich fens, characterized by the highest pH values, naturally constitute habitat for diverse calcicolous species such as *Carex atrofusca*, *C. aurea* Nutt., *C. bicolor* All., *C. capillaris*, *C. concinna*, *C. chordorrhiza* Ehrh. ex L. f., *C. diandra* Schrank, *C. gynocrates* Wormsk. ex Drejer, *C. interior*, *C. leptalea* Wahlenb. subsp. *leptalea*, *C. livida* (Wahlenb.) Willd.,



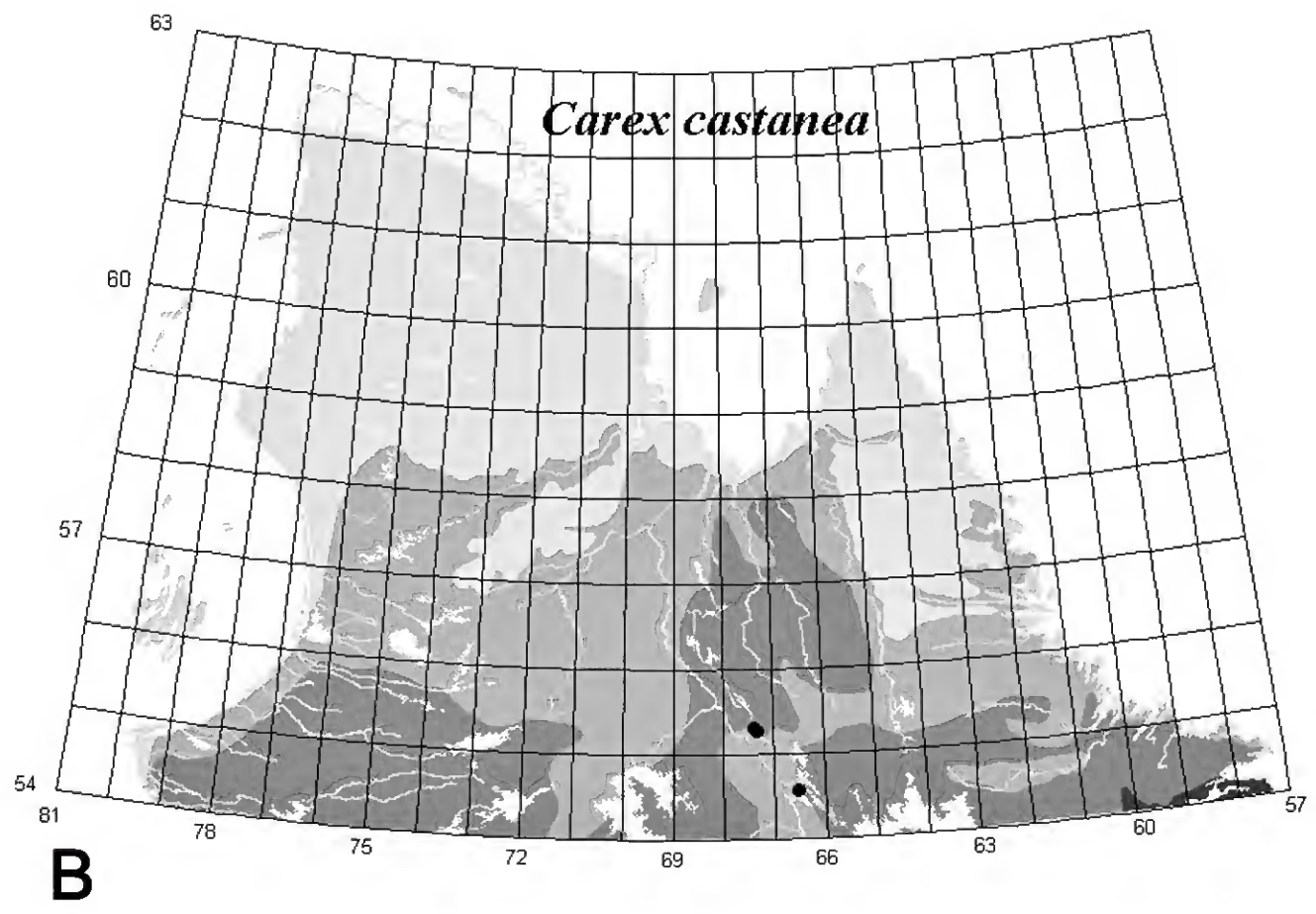


Figure 2. —A. *Carex bigelowii* in Quebec-Labrador north of 54°N. —B. *Carex castanea* in Quebec-Labrador north of 54°N. Maps used with permission of the Northern Québec-Labrador Flora project.

C. microglochin, *C. tenuiflora* Wahlenb., and *C. vaginata* Tausch. Other peatlands, especially in the forest tundra close to the tree line, are more acidic (Fig. 3B). Characteristic *Carex* species are: *C. aquatilis* var. *aquatilis*, *C. bigelowii* subsp. *bigelowii*, *C. brunnescens* (Pers.) Poir. s.l., *C. echinata* Murr. subsp. *echinata*, *C. exilis* Dewey, *C. heleonastes* L. f., *C. limosa* L., *C. magellanica* subsp. *irrigua*, *C. marina* Dewey, *C. michauxiana*, *C. oligosperma* Michx., *C. rariflora*, *C. rotundata*, *C. saxatilis*, and *C. williamsii* Britton. Acidic *Sphagnum* bogs are almost absent from the study area. Generally, they are restricted to the margins

of fens (Payette, 2001b) or around extensive lakes (Payette, 1988). They are home to *C. limosa*, *C. pauciflora* Lightf., and *C. trisperma* Dewey. In the open woodland subzone, various wetland communities are the common habitat for *C. atratiformis* Britton, *C. brunnescens* s.l., *C. disperma* Dewey, *C. leptalea* subsp. *leptalea*, *C. leptonervia*, *C. pauciflora*, *C. stylosa*, *C. trisperma*, and *C. vaginata*.

Water bodies are found by the thousands at these latitudes, primarily due to recent glacial ice action, permafrost soils, and severe climatic conditions. Shores of permanent or temporary pools or ponds (Fig. 3C) are suitable for most of the common species such as *Carex aquatilis* var. *aquatilis*, *C. arcta* Boott, *C. bicolor*, *C. bigelowii* subsp. *bigelowii*, *C. canescens* s.l., *C. capillaris*, *C. fuliginosa*, *C. holostoma*, *C. lenticularis* Michx. var. *lenticularis*, *C. membranacea*, *C. microglochin*, *C. norvegica* subsp. *norvegica*, *C. rariflora*, *C. rostrata* Stokes, *C. rufina* Drejer, *C. saxatilis*, *C. stylosa*, *C. utriculata* Boott, *C. vesicaria* L., *C. viridula* Michx. subsp. *viridula*, and *C. williamsii*. The rather rare *C. lapponica* and *C. michauxiana* also are found in such habitats.

Lakeshore species differ in arctic and boreal environments. Characteristic species of arctic lakeshores are: *Carex membranacea*, *C. rotundata*, *C. rufina*, and *C. saxatilis*, whereas along boreal lakeshores, the common species are *C. aquatilis* var. *aquatilis*, *C. chordorrhiza*, *C. diandra*, *C. oligosperma*, *C. rostrata*, *C. saxatilis*, and *C. utriculata*. *Carex michauxiana* is only occasional on boreal lakeshores.

Shores of small streams, brooks, and rivulets provide sheltered conditions for *Carex adelostoma*, *C. buxbaumii* Wahlenb., *C. chordorrhiza*, *C. echinata* subsp. *echinata*, *C. gynocrates*, *C. holostoma*, *C. leptalea* subsp. *leptalea*, *C. macloviana*, *C. magellanica* subsp. *irrigua*, *C. norvegica* subsp. *norvegica*, *C. rariflora*, *C. rostrata*, *C. rufina*, *C. saxatilis*, *C. stylosa*, *C. tenuiflora*, *C. vaginata*, and *C. williamsii*. The *Carex* flora of river shores seems to be more diversified under boreal conditions than arctic, and includes *C. bicolor*, *C. canescens* subsp. *canescens* and subsp. *disjuncta*, *C. castanea*, *C. conoidea*, *C. echinata* subsp. *echinata*, *C. garberi*, *C. lenticularis* var. *lenticularis*, *C. leptonervia*, *C. scirpoidea* subsp. *scirpoidea*, and *C. viridula* subsp. *viridula*.

Mesic habitats are widespread in all areas: slopes, upper shores, terraces, river flats, and ledges, where the following species are likely to be found: *Carex atratiformis*, *C. bigelowii* subsp. *bigelowii*, *C. brunnescens* s.l., *C. capillaris*, *C. deflexa* Hornem. var. *deflexa*, *C. eburnea*, *C. fuliginosa*, *C. macloviana*, *C. norvegica* subsp. *inferalpina* (Wahlenb.) Hultén and subsp. *norvegica*, *C. petricosa* var. *misandroides*, *C. rupestris* All., *C. scirpoidea* subsp. *scirpoidea*, and *C. supina* Willd. ex Wahlenb. subsp. *spaniocarpa* (Steud.) Hultén.

Drier conditions are associated with glacial and postglacial deposits (coarse fluvial sediments, eskers, etc.), active geomorphic features (dunes, rocky talus, etc.), and outcrops. Species growing on dunes and sand deposits are *Carex adusta*, *C. capitata*, *C. crawfordii*, *C. deflexa* var. *deflexa*, *C. foenea* Willd., *C. nardina* Fries, and *C. praticola*. On gravelly deposits and eskers, *C. bigelowii* subsp. *bigelowii*, *C. glacialis* Mack., and *C. supina* subsp. *spaniocarpa* are frequent, while *C. bigelowii* subsp. *bigelowii*, *C. capitata*, and *C. nardina* grow on rocky outcrops. Calciphilic species, typically occurring on calcareous outcrops (Fig. 3D), are *C. concinna*, *C. eburnea*, *C. petricosa* var. *misandroides*, and *C. rupestris*. The last four species, as well as *C. castanea*, are considered to be obligate calciphiles in the study area (Appendix 1).

Due to severe climatic conditions encountered in the study area, periglacial (or frost-induced) environments, such as patterned ground, snow beds, and mud boils, are widespread (Rousseau, 1968). Snow beds are located on slopes, at the bases of cliffs, at the edges of rivers, lakes, etc. *Carex lachenalii* Schkuhr is confined to this type of habitat, but other species are able to inhabit snow beds as well: *C. bigelowii* subsp. *bigelowii*, *C. brunnescens* subsp. *brunnescens*, *C. deflexa* var. *deflexa*, *C. fuliginosa*, *C. holostoma*, *C. membranacea*, *C. rariflora*, *C. rotundata*, *C. scirpoidea* subsp. *scirpoidea*, and *C. vaginata*. Mud boils usually are found close to the tree line and in arctic settings. They represent recent openings in tundra conditions in the otherwise continuous tundra vegetation, and favor the establishment of pioneer species such as *C. bicolor*, *C. capillaris*, *C. gynocrates*, *C. williamsii*, and widespread species such as *C. aquatilis* var. *aquatilis* and *C. bigelowii* subsp. *bigelowii*.

Habitat diversity of *Carex* taxa in the study area was briefly analyzed from the data of Appendix 1 and Table 1. As expected, taxa of humid habitats

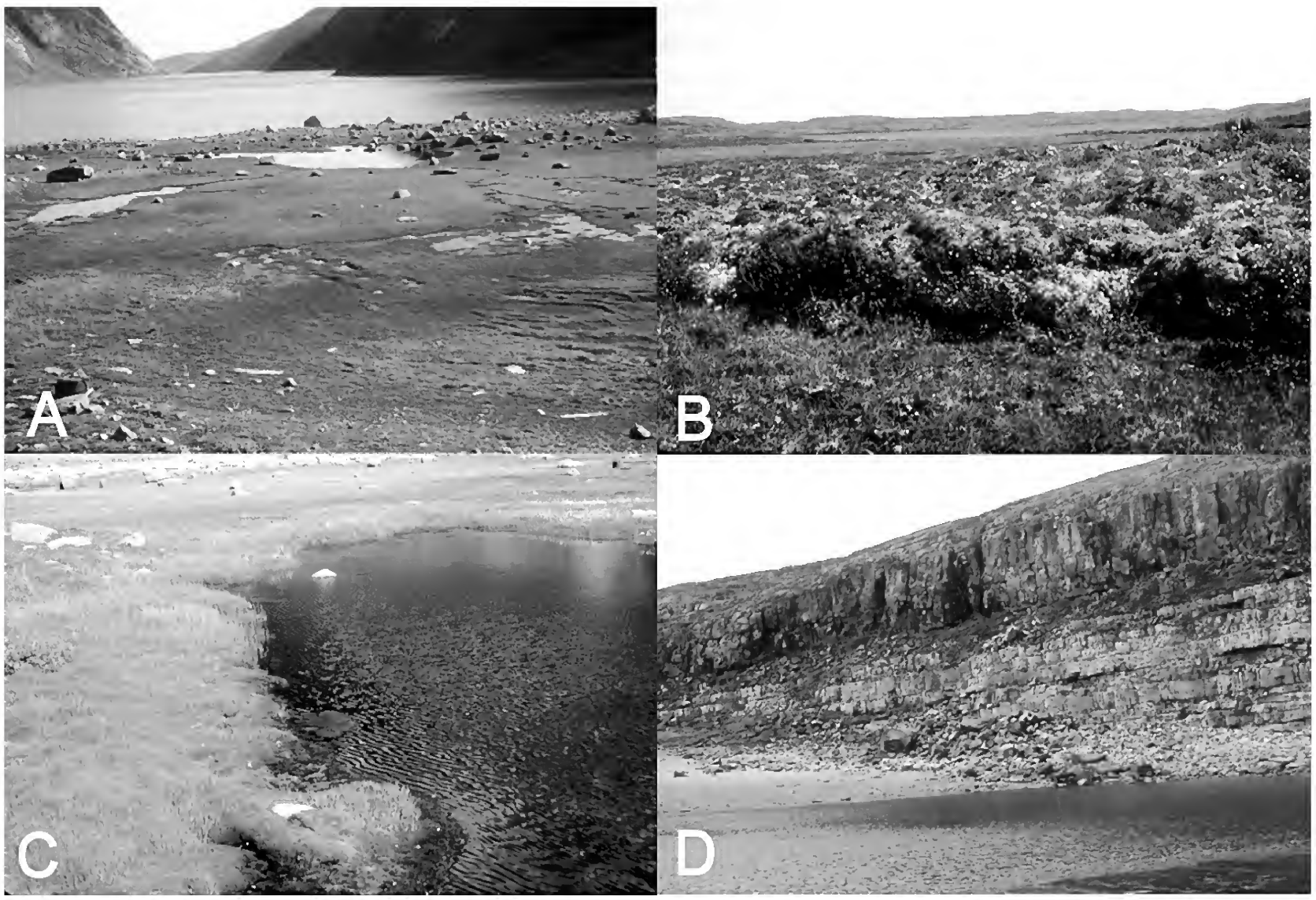


Figure 3. Selection of *Carex* habitats in Quebec-Labrador north of 54°N. —A. Salt marsh with *C. subspathacea*, Havre Douglas, southwest arm, Quebec (61°57′N–72°50′W), 31 July 1981. —B. Palsa fen, Chavigny lake area, Quebec (58°12′N–75°08′W), 27 July 1982. —C. High tide pool with *C. rariflora*, Havre Douglas, southwest arm, Quebec, 31 July 1981. —D. Dolomite and basalt cliffs, Bill-of-Portland Island, Hudson Bay, Nunavut Territory (55°22′N–77°05′W), 7 July 1982.

predominate. They are present in wetlands, including peatlands and salt marshes (46: 58%) or on various shores (42: 52%), such as river shores, lake shores, and shores of various small streams and other water bodies. Taxa occurring in wetlands or shores total 63 (77%). On the other hand, taxa of mesic (17: 21%) and dry (13: 16%) habitats are less important. Most of the taxa occur in only one of these categories, but some may occur in two categories, and *C. bigelowii* is found in every type of drainage. Its broad ecological tolerance is certainly one of the reasons for its abundance in the study area (Fig. 2A).

Fewer taxa occur in specialized habitats. Twelve (15%) are found in snow beds and six (8%) in mud boils. Few obligate calciphiles occur (5: 6%) and they are *Carex castanea*, *C. concinna*, *C. eburnea*, *C. petricosa* var. *misandroides*, and *C. rupestris*. Other calcicolous taxa are found in rich fens, for instance, and in other types of habitats, but they have not been considered here in this calculation because more data are needed to determine their soil preference in the study area.

TAXONOMIC PROBLEMS

In the study area, 97 *Carex* taxa are recognized, including 16 hybrids. Forty (46%) of the 97 taxa require some degree of taxonomic clarification (Appendix 1; Table 1). Eighteen species (22%) form closely related species complexes, while infraspecific variants and natural hybrids account for 5% and 19% of the taxonomic problems, respectively. The following comments are divided along these three lines. Some new data are presented concerning *C. lapponica* and *C.* ×*flavicans*.

Species complexes

Eighteen species belong to circumpolar species complexes. Relatively little time (ca. 6000 YBP) has passed since the deglaciation of the northern Quebec-Labrador Peninsula (Richard et al., 1982; Dyke & Prest, 1987). Plant colonization occurred from vegetation situated at the southern edge of the glaciers (Richard, 1985; Gajewski et al., 1996). Nevertheless, contact between coastal arctic and boreal zones especially along the coast of southern Hudson Bay and northern James Bay is where arctic and boreal elements of the same species complex occur. Thus anomalous juxtapositions were created. Specific problems are briefly summarized.

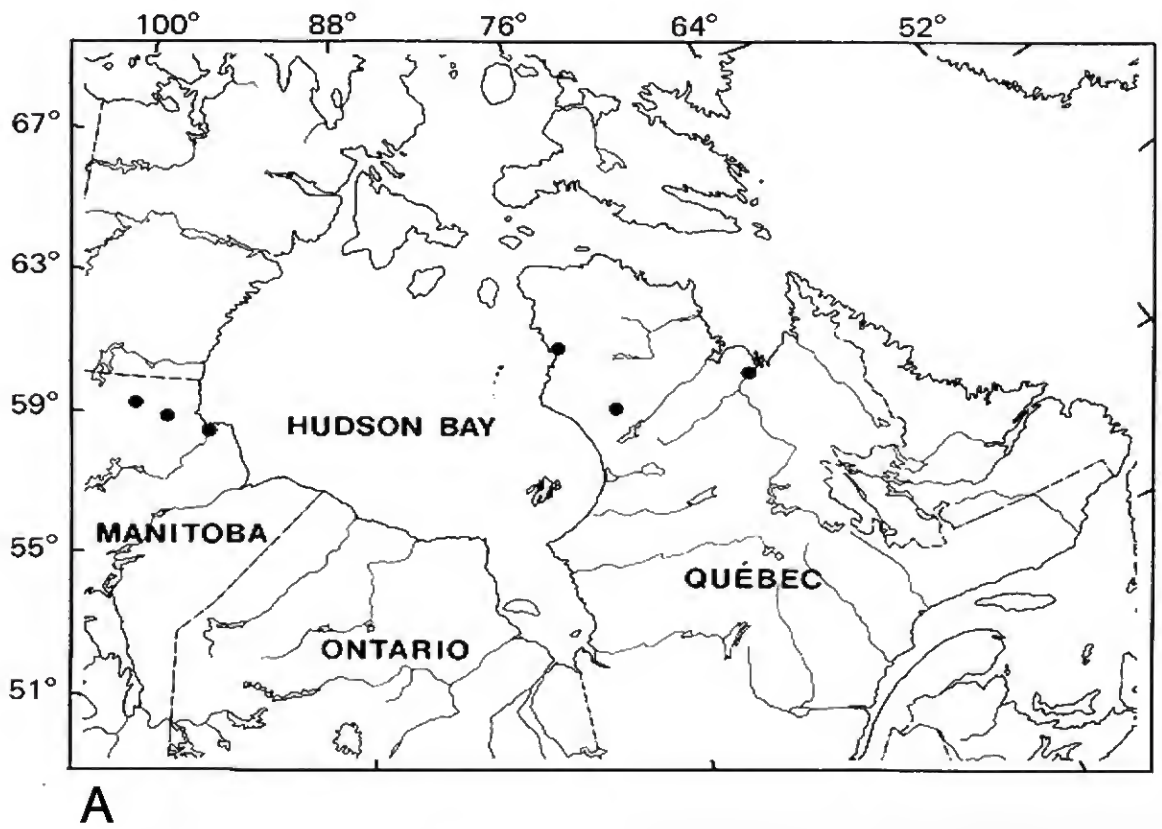
In section *Glareosae*, the *Carex glareosa* group encompasses four species: *C. glareosa*, *C. heleonastes*, *C. lachenalii*, and *C. marina*. *Carex glareosa* (seashores) and *C. lachenalii* (snow beds) have restricted habitat requirements and distinctive morphological characters. In comparison, *C. heleonastes* and *C. marina* both occur in coastal fens and are more difficult to distinguish (Böcher, 1952; Toivonen, 1981a, 2002). Their phytogeography is different: *C. heleonastes* is boreal and *C. marina* is arctic (Hultén & Fries, 1986). Both species are sympatric at the southernmost arctic zone along the James Bay coast at about 54°N. As no intermediate specimens have been found in this area, they are likely two different species.

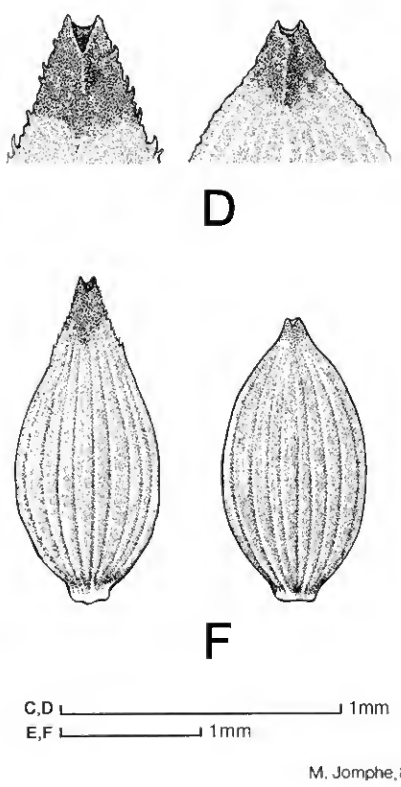
Within section *Racemosae*, *Carex adelostoma* and *C. buxbaumii* are closely related. They both occur in the study area, the first being restricted to a relatively narrow zone in the low-arctic region while the other is boreal and extends into the temperate zone. While they are sympatric in the study area (*C. adelostoma* occurs from 55°N to almost 59°N and *C. buxbaumii* from 54°N to 57°N), they occupy different vegetation subzones. *Carex adelostoma* is exclusively found in shrub and forest tundra subzones, whereas *C. buxbaumii* is primarily confined to the lichen woodland subzone. They have been treated in various ways by caricologists, either as different species or lower taxa (Raymond, 1950, 1951; Murray, 2002a), but rarely as conspecific (e.g., Boivin, 1992). They share the same high chromosome numbers (Cayouette, 1997) and are characterized by significant meiotic irregularities. Nevertheless, their pollen stainability is high. Usually, they can be separated by good morphological characters, but no recent taxonomic work has addressed variation at the circumhemispheric level. Relationships with other taxa such as *C. hartmanii* Cajander require further clarification.

There are three schools of thought regarding the North American *Carex atratiformis*, also in section *Racemosae*. (1) Most recent authors treat it as a taxon different from the European *C. atrata* L. (e.g., Murray, 2002a). However (2), Boivin (1992) placed *C. atratiformis* in synonymy with *C. atrata*. Others (3) claim that both *C. atrata* and *C. atratiformis* are found in the study area (Raymond, 1950, 1951; Scoggan, 1978). A preliminary examination of specimens of *C. atratiformis* from the study area and of specimens of *C. atrata* from Greenland and Northern Europe has confirmed that the two taxa are morphologically similar. Even if most specimens seem to be separable by a combination of characters, some are not, indicating the need for additional study.

The relationship of *Carex media* R. Br. ex Richardson and *C. norvegica*, again in section *Racemosae*, has long been considered a very difficult problem. According to Hultén and Fries (1986) and Murray (2002a), *C. norvegica* is arctic-alpine and amphi-Atlantic in range, whereas *C. media* is circumboreal. In the northeast, proper identification of *C. norvegica* in the arctic zone and *C. media* in the southern boreal region, such as in the Gaspé Peninsula lowlands, Quebec, is straightforward. However, in the study area, between 54°N and tree line, both *C. media* and specimens intermediate with *C. norvegica* occur in forest tundra (P. Morisset, pers. comm.), and such specimens are difficult to identify. The same situation occurs in Northern Europe. Subspecific subdivision has been recommended (D. Murray, pers. comm.). For now, *C. norvegica* is considered as subspecies *norvegica* and *C. media* as *C. norvegica* subsp. *inferalpina* (Appendix 1), but a taxonomic study, using various lines of evidence, is needed to clarify the situation.

In section *Chlorostachyae* Tuck. ex Meinsh., three levels of an apparent polyploid complex are represented in the study area: the diploid *Carex williamsii* ($2n = 18$), the tetraploid *C. krausei* ($2n = 36$), and the hexaploid *C. capillaris* s.l. ($2n = 54$) (Löve et al., 1957; Ball, 2002a). No taxonomic problem is apparent for *C. williamsii*, but the other two taxa have been treated variously (Löve et al., 1957; Egorova, 1999).





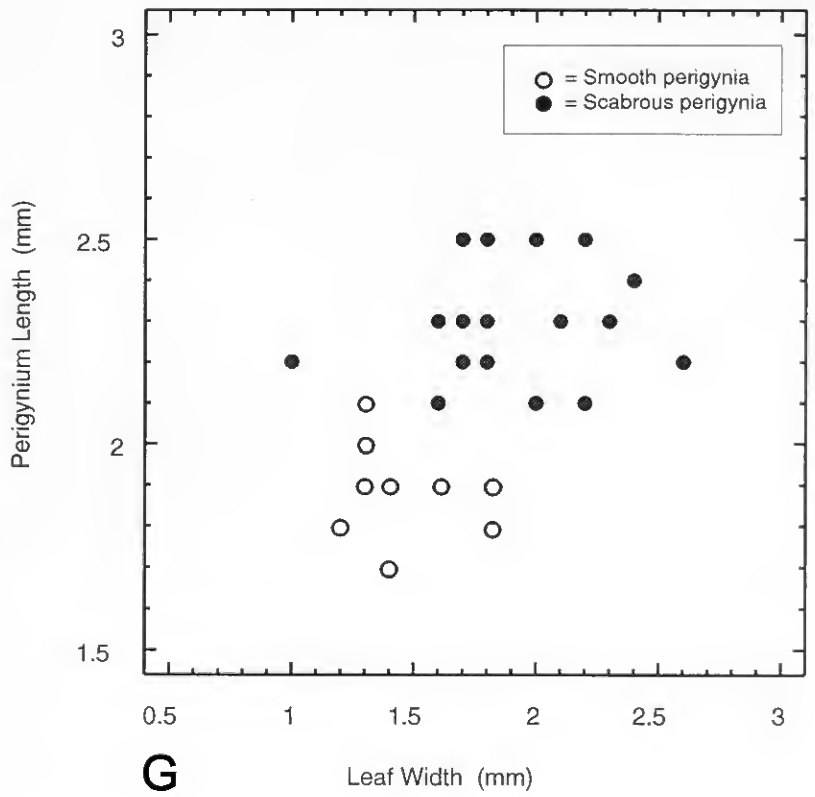


Figure 4. —A. *Carex lapponica* in northeastern Canada. —B. Inflorescence of *C. lapponica* (*J82-191* DAO). —C, E. Perigynium of *C. canescens* subsp. *canescens*. —D, F. Perigynium of *C. lapponica*. —G. Perigynium length plotted against leaf width for 10 specimens each of *C. canescens* subsp. *canescens* and subsp. *disjuncta* (solid circles) and nine of *C. lapponica* (open circles).

Among the short-beaked species of *Carex* sect. *Vesicariae*, the two tristigmatic species, *C. membranacea* and *C. rotundata*, have long been considered difficult to separate. Recent investigations by Ford et al. (1991, 1993) and Reznicek and Ford (2002) have now demonstrated appreciable differences using molecular and morphological data. Among the herbarium specimens examined for his studies and for the Flora of North America project, B. Ford (pers. comm.) has noticed that the discrimination between the two species is sometimes obscure in material from Quebec-Labrador.

Both *Carex rostrata* and *C. utriculata* (section *Vesicariae*) occur in the study area and are now considered circumboreal (Reznicek & Ford, 2002). Until recently, they have not been correctly distin-

guished in North America. Reznicek (1985; in Griffiths, 1989) was the first to report their presence in North America, and to provide key characters for separating the taxa. Recent evidence presented by Ford et al. (1993) and Reznicek and Ford (2002) have confirmed the presence of two species.

In section *Capituligerae* Kük., there has long been a debate whether one or two taxa should be recognized in the Northern Hemisphere: *Carex arctogena* Harry Sm. and *C. capitata* (Murray, 2002b). Recent studies in Scandinavia have shown that *C. arctogena* is different in many aspects from *C. capitata*, even though most morphological characters overlap (Reinhammar & Bele, 2001). Both *C. arctogena* and *C. capitata* have been attributed to the study area, either at the specific level or as infraspecific taxa (Smith, 1940; Raymond, 1949; Scoggan, 1978; Hultén & Fries, 1986; Reinhammar & Bele, 2001).

Carex lapponica *in northeastern Canada*

In section *Glareosae*, *Carex lapponica* (Fig. 4B) is morphologically similar to *C. canescens* s.l. Its occurrence in North America, especially in the northeast, has long been misunderstood (Toivonen, 1981a). For instance, the map of *C. lapponica* in Porsild and Cody (1980) is generally correct in the western part of the continent, but is inaccurate in the central and eastern region. Only 12 specimens proved to be referable to *C. lapponica* with three occurrences in Quebec (five sites) and three in northern Manitoba (Fig. 4A). Complete citations are given in Appendix 2. Plants from all the other sites in eastern and central North America are referable to *C. canescens*.

Revisions to *Carex lapponica* were based on the morphological characters suggested by Toivonen (1981a, 2002). Those most useful for separating it from *C. canescens* s.l. were tested on a selection of specimens from northeastern North America. Almost all specimens of *C. lapponica* found in this region (9) were used for this study and an equivalent number of specimens of *C. canescens* s.l. The results were consistent with the observations of Toivonen (1981a). *Carex lapponica* has perigynia (1.5–)1.7–2.1 mm long (2.1–2.5[–3.0] mm in *C. canescens*) (Fig. 4E, F), with upper margins smooth and abruptly contracted into a short beak (scabrous, sometimes only with a few prickly hairs, and tapering or contracted into a short beak in *C. canescens*) (Fig. 4C, D), and leaves 1.2–1.8 mm wide ([1.0–]1.6–2.6–4.0] mm in *C. canescens*). A plot diagram (Fig. 4G) of these differences indicates a clear distinction between *C. lapponica* and *C. canescens* s.l.

Carex lapponica is considered to be rare in Quebec (Lavoie, 1992; Labrecque & Lavoie, 2002), in Yukon Territory (Douglas et al., 1981, as *C. canescens* var. *subloliacea* Laest.), and in British Columbia (Douglas et al., 2002). It was not included in the list of rare plants of Manitoba (White & Johnson, 1980), but as only three localities have been reported in the province (Fig. 4A), it should be added to the list.

As mentioned above, *Carex lapponica* seems to be confined to a narrow strip along the high-boreal zone, at least in northeastern Canada, and is likely overlooked and rarely collected as a result of both limited occurrence and similarity to *C. canescens* subsp. *canescens*.

Infraspecific variation

In section *Glareosae*, each of the boreal species *Carex brunnescens* and *C. canescens* has a southern subspecies in eastern North America that is mainly restricted to the southern part of the study area. Like subspecies *brunnescens*, *C. brunnescens* subsp. *sphaerostachya* (Toivonen, 1981a, 2002) is considered circumboreal (Appendix 1), whereas *C. canescens* subsp. *disjuncta* is considered temperate and endemic to northeastern North America (Toivonen, 1981b). Consistent with the observations of Toivonen (1981b, 2002), in northern Quebec-Labrador, within each species, the subspecies are not always separable.

Natural hybridization

In North America, natural hybridization within *Carex* appears to be more prevalent in glaciated areas than in unglaciated ones (Cayouette & Catling, 1992). It is thus not surprising that many reports of *Carex* hybrids are known from the study area. Some of the reports have been revised to orthospecies or other nothospecies (Cayouette, 1990; Cayouette & Catling, 1992; Ford et al., 1993), but 18 taxa remain that are considered hybrids or of hybrid origin (Appendix 1). In a few cases, further investigation is still required.

Sections involved in hybridization are *Glareosae*, *Phacocystis*, *Racemosae*, and *Vesicariae*. One intersectional hybrid is reported: *Carex* ×*langeana*

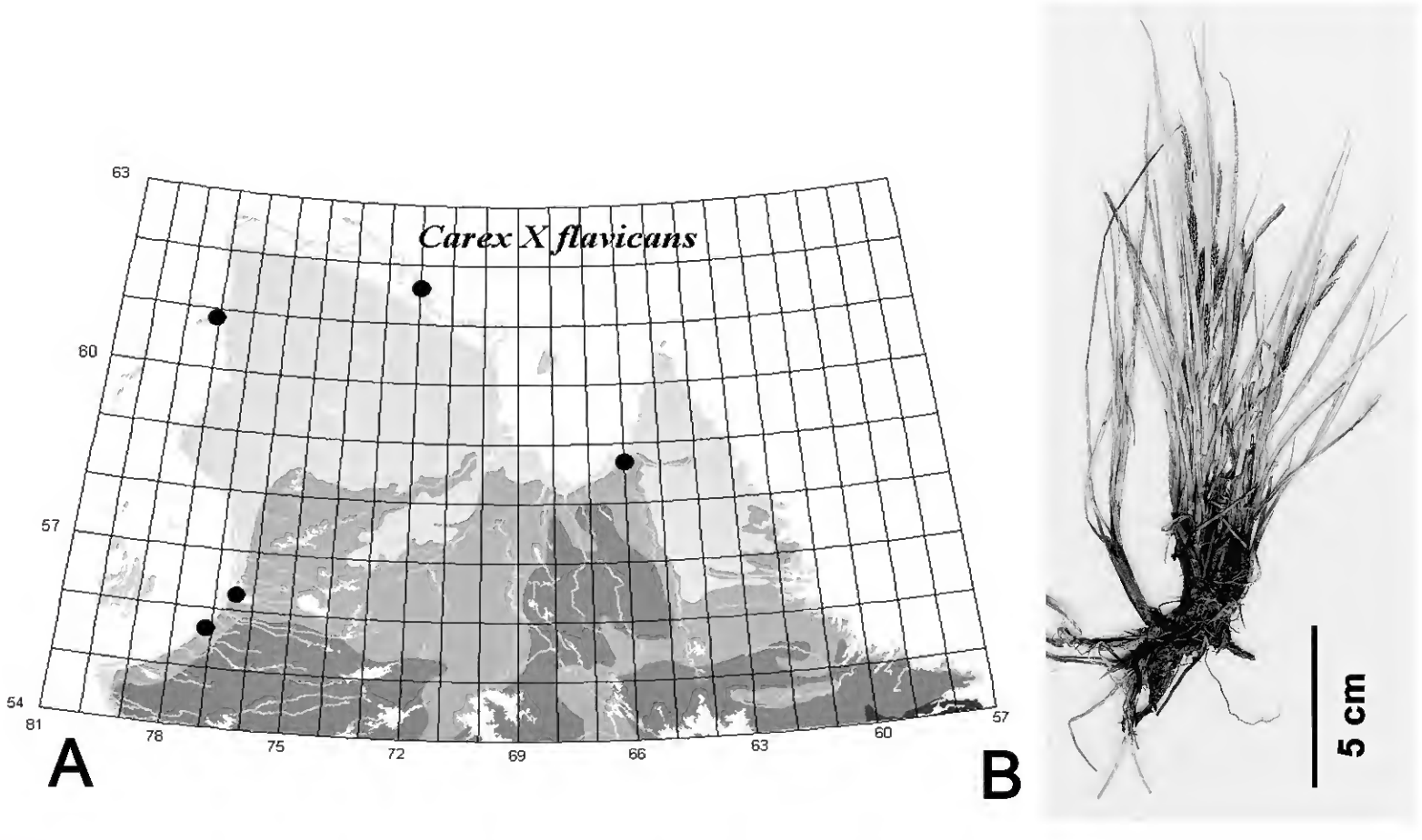


Figure 5. —A. *Carex* ×*flavicans* in Quebec-Labrador north of 54°N. —B. *Carex* ×*flavicans* (*J82-231* DAO). Map used with permission of the Northern Québec-Labrador Flora project.

Fernald [*C. gynocrates* (sect. *Physoglochin* Dumort.) × *C. maritima* (sect. *Foetidae* (Tuck. ex L. H. Bailey) Kük.)]. Species most involved in hybrid combinations are *C. aquatilis* (five), *C. paleacea*, *C. salina*, and *C. saxatilis* (three each).

Two species of hybrid origin are present in the study area, the coastal *Carex recta* and *C. salina*. Their parental species are *C. aquatilis* × *C. paleacea* and *C. paleacea* × *C. subspathacea*, respectively (Cayouette & Morisset, 1985; Standley, 1990; Cayouette & Catling, 1992; Standley et al., 2002). They are considered to be stabilized hybrids because they have high pollen fertility, set seeds, and are relatively abundant in the sympatric zone occupied by their putative parents. In the study area both taxa occur at the northeastern limit of their range in North America and do not grow beyond the range of their parents.

Another hybrid (*Carex aquatilis* × *C. subspathacea* = *Carex* ×*flavicans*), superficially similar to *C. salina*, has been found to be widespread in the study area and in northeastern North America (Fig. 5B). This taxon seems to replace *C. salina* beyond its northern limit and represents most of the plants considered by Polunin as "*C. salina* transitional to *aquatilis* var. *stans*" (Polunin, 1940: 134). Key characters of *C.* ×*flavicans* are given in Cayouette and Morisset (1985: table 1). Seven populations (five occurrences) now occur in the study area: Hudson Bay, Ungava Bay, and Hudson Strait (Fig. 5A). All known collections are cited in Appendix 2.

Outside the study area, *Carex* ×*flavicans* is known from various regions: James Bay in Ontario (three sites), Hudson Bay in Manitoba (many sites in the Churchill area), Southampton Island, Devon Island, and Baffin Island in Nunavut Territory (Cayouette & Catling, 1992).

This hybrid is not only widespread, but frequently forms extensive populations in coastal ponds, above high tide, in the Churchill area, Manitoba, especially close to nesting grounds of Lesser Snow Geese (Kotanen & Jefferies, 1989a, b), and also around Manitounuk Sound, Quebec (Deshaye & Cayouette, 1988). Like other hybrids involving *Phacocystis* species, the pollen stainability and seed set of *Carex* ×*flavicans* are high. Meiotic irregularities are minor (Cayouette & Morisset, 1985) and comparable to those of *C. recta* and *C. salina*, and even to some cytotypes of *C. aquatilis* (Cayouette & Morisset, 1986). For these reasons, *C.* ×*flavicans* seems to represent another species of

hybrid origin in North America within section *Phacocystis*, along with *C. recta*, *C. salina*, and *C. vacillans* Drejer (*C. nigra* (L.) Reichard × *C. paleacea*) (Cayouette & Catling, 1992; Cayouette, in Standley et al., 2002).

It is interesting to note that natural hybridization is not restricted to the genus *Carex* in the study area, but also occurs in other groups of vascular plants, such as *Andromeda* L., *Cornus* L. (Cayouette, 1986b), *Ranunculus* L. (Cody et al., 1988; Cayouette et al., 1997), *Dupontia* R. Br., and *Poa* L. (Darbyshire et al., 1992; Cayouette & Darbyshire, 1993).

Conclusion

Herbarium specimens provide good coverage of the *Carex* flora of Quebec-Labrador north of 54°N. This survey has greatly improved our knowledge of the diversity of *Carex* species, in terms of numbers of taxa, range, abundance, and relative frequency within each taxon's respective habitats. While this survey highlighted most of the taxonomic problems found in the region, a few problems remain and should be examined more extensively. New information on the rare *C. lapponica* in northeastern North America pinpointed its occurrences in two Canadian provinces. *Carex* ×*flavicans* appears to be another stabilized hybrid in section *Phacocystis*. Our results suggest that it is more widespread than previously thought.

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Appendix 1

List of *Carex* taxa of Quebec-Labrador north of 54°N and their characteristics. Data in brackets were excluded from the analysis.

Number	Sections	Species	Subspecies, varieties, hybrid parentage	Phytogeography [1]	Abundance [2]	Habitats [3]	Taxonomic problems [4]
1	*Heleoglochin* Dumort.	*diandra* Schrank		b; cb	2	w, s	—
2	*Dispermae* Ohwi	*disperma* Dewey		b; cb	2	w	—
3	*Chordorrhizae* (Heuff.) Meinsh.	*chordorrhiza* Ehrh. ex L. f.		b; cb	2	w, s	—
4	*Physoglochin* Neck. ex Dumort.	*gynocrates* Wormsk. ex Drejer		b; na-ea	2	w, s, mb	—
5	*Foetidae* (Tuck. ex L. H. Bailey) Kük. in A. H. G. Engler	*maritima* Gunnerus		a*; cp	2	c, m, d	—
		×*langeana* Fernald	*gynocrates* × *maritima*		[1]	[c, w, m]	h
6	*Glareosae* G. Don in J. C. Loudon	*arcta* Boott		b; na	2	s	—
		brunnescens (Pers.) Poir. in J. Lamarck et al.	subsp. *brunnescens*	b; cb	2	w, m, sb	iv
		brunnescens (Pers.) Poir. in J. Lamarck et al.	subsp. *sphaerostachya* (Tuck.) Kalela	b; cbd	2	w, m	iv
		canescens L.	subsp. *canescens*	b*; cb	2	s	iv
		canescens L.	subsp. *disjuncta* (Fernald) Toivonen	t; nea	1	s	iv
			canescens × *trisperma*		[1]	[w]	h
		glareosa Wahlenb.	subsp. *glareosa*	a; cpd	2	c, w, m	sc
		heleonastes L. f.		b; cbd	2	w	sc
		lachenalii Schkuhr		aa; cp	2	sb	sc
		lapponica O. Lang		hb; cbd	1	s	sc
		mackenziei V. I. Krecz. in V. L. Komarov et al.		b; cbd	2	c, w	—
		marina Dewey		a; cp	2	w	sc
		tenuiflora Wahlenb.		b; cb	2	w, s	—
		trisperma Dewey		b; na	2	w	—
		ursina Dewey		a; cp	2	c, w	—
7	*Stellulatae* Kunth	*echinata* Murr.	subsp. *echinata*	b; cbd	2	w, s	—
		exilis Dewey		b; nea	2	w	—
		interior L. H. Bailey		t; na	1	w	—
8	*Ovales* Kunth	*adusta* Boott in W. J. Hooker		b; na	1	d	—
		crawfordii Fernald		t; na	1	d	—
		foenea Willd.		b; na	2	d	—
		macloviana d'Urv.		aa*; co	1	s, m	—
		praticola Rydb.		b; na	2	c, d	—

9	*Phacocystis* Dumort.	*aquatilis* Wahlenb.	var. *aquatilis*	b; cb	2	w, s, mb	—
		bigelowii Torr. ex Schwein.	subsp. *bigelowii*	aa; cpd	3	w, s, m, d, sb, mb	—
		×*exsalina* Lepage	*bigelowii* × *paleacea*		[1]	[c, w]	h
		×*flavicans* (F. Nyl.) F. Nyl.	*aquatilis* × *subspathacea*		[1]	[c, w]	h
		×*grantii* A. Benn.	*aquatilis* × *recta*		[1]	[c, w]	h
		lenticularis Michx.	var. *lenticularis*	b; na	2	s	—
		×*limula* Fries	*aquatilis* × *bigelowii*		[1]	[w]	h
		×*mendica* Lepage	*recta* × *salina*		[1]	[c, w]	h
		×*neofilipendula* Lepage	*aquatilis* × *paleacea*		[1]	[c, w]	h
		paleacea Schreb. ex Wahlenb.		b; amp	2	c, w	—
		recta Boott in W. J. Hooker		b; amp	1	c, w	h
		rufina Drejer		a; amp	1	s	—
		salina Wahlenb.		b; amp	2	c, w	h
		×*subpaleacea* J. Cay.	*paleacea* × *salina*		[1]	[c, w]	h
		×*subsalina* Lepage	*aquatilis* × *salina*		[1]	[c, w]	h
		subspathacea Wormsk. in G. C. Oeder et al.		a; cp	2	c, w	—
10	*Racemosae* G. Don in J. C. Loudon	*adelostoma* V. I. Krecz. in V. L. Komarov et al.		la; cpd	1	s	sc
		atratiformis Britton		b; na	2	m	sc
		buxbaumii Wahlenb.		b; cbd	2	s	sc
		holostoma Drejer		a; cpd	2	w, s, sb	—
		norvegica Retz.	subsp. *inferalpina* (Wahlenb.) Hultén	b; cb	2	m	sc
		norvegica Retz.	subsp. *norvegica*	aa; amp	3	s, m, sb	sc
		×*patuensis* Lepage (to be confirmed)	*atratiformis* × *saxatilis*	[1]	[s]	h	
		×*quirponensis* Fernald	*atratiformis* × *norvegica*		[1]	[s, m, d]	h
		stylosa C. A. Mey.		b; co	2	w, s	—
11	*Limosae* (Heuff.) Meinsh.	×*firmior* (Norman) Holmberg	*limosa* × *rariflora*		[1]	[w]	h
		limosa L.		b; cb	2	w	—
		magellanica Lam. in J. Lamark et al.	subsp. *irrigua* (Wahlenb.) Hiitonen	b*; cb	2	w, s	—
		rariflora (Wahlenb.) Sm. in J. E. Smith and J. Sowerby		a; cp	3	w, s, sb	—
12	*Bicolores* (Tuck. ex L. H. Bailey) Rouy	*aurea* Nutt.		b; na	2	w	—
		bicolor All.		aa; cp	2	w, s, mb	—
		garberi Fernald		b; na	1	s	—
13	*Paniceae* G. Don in J. C. Loudon	*livida* (Wahlenb.) Willd.		b; cbd	2	w	—
		vaginata Tausch		b; cb	2	w, s, sb	—
14	*Laxiflorae* (Kunth) Mackenzie in N. L. Britton et al.	*leptonervia* (Fernald) Fernald		t; nea	1	w, s	—
15	*Griseae* (L. H. Bailey) Kük. in H. G. A. Engler	*conoidea* Willd.		t; nea	1	s	—
16	*Hymenochlaenae* (Drejer) L. H. Bailey in J. M. Coulter	*castanea* Wahlenb.		b; nea	1	ca, s	—
17	*Chlorostachyae* Tuck. ex Meinsh.	*capillaris* L.		aa; cp	3	w, s, m, mb	sc
		krausei Boeckeler		a; cpd	1	c, w	sc
		williamsii Britton		a; na-ea	2	w, s, mb	—

Appendix 1. Continued.

Number	Sections	Species	Subspecies, varieties, hybrid parentage	Phytogeography [1]	Abundance [2]	Habitats [3]	Taxonomic problems [4]
18	*Aulocystis* Dumort.	*fuliginosa* Schkuhr		aa; cp	2	w, s, m, sb	—
		petricosa Dewey	var. *misandroides* (Fernald) B. Boivin	b; nea	1	ca, m	—
19	*Chartoteuchium* (Börner) V. I. Krecz. in V. L. Komarov et al.	*atrofusca* Schkuhr		aa; cp	2	w	—
20	*Porocystis* Dumort.	*pallescens* L.		t; amp	1	—	—
21	*Vesicariae* (Heuff.) J. Carey	*membranacea* Hook. in G. F. Lyon		a; na-ea	2	w, s, sb	sc
		oligosperma Michx.		b; nea	2	w, s	—
		rostrata Stokes in W. Withering		b; cb	2	s	sc
		rotundata Wahlenb.		a; cp	2	w, s, sb	sc
			rotundata × *saxatilis*		[1]	[w]	h
		saxatilis L.		aa; cp	3	w, s	sc
			saxatilis × *utriculata*		[2]	[s]	h
		×*stenolepis* Less.	*saxatilis* × *vesicaria*		[1]	[s]	h
		utriculata Boott in W. J. Hooker		b; cb	2	s	sc
		vesicaria L.		b; cb	2	s	—
22	*Rostrales* Meinsh.	*michauxiana* Boeckeler		b; nea-ea	1	w, s	—
23	*Ceratocystis* Dumort.	*viridula* Michx.	subsp. *viridula* var. *viridula*	b; cb	2	s	—
24	*Leucoglochin* Dumort.	*microglochin* Wahlenb.		aa*; cpd	2	w, s	—
		pauciflora Lightf.		b; cb	2	w	—
25	*Acrocystis* Dumort.	*deflexa* Hornem.	var. *deflexa*	b; na	2	m, d, sb	—
26	*Clandestinae* G. Don in J. C. Loudon	*concinna* R. Br. in J. Franklin et al.		b; na	1	ca, w	—
27	*Scirpinae* (Tuck.) Kük. in H. G. A. Engler	*scirpoidea* Michx.	subsp. *scirpoidea*	aa; na-ea	3	s, m, sb	—
28	*Albae* (Asch. & Graebn.) Kük. in H. G. A. Engler	*eburnea* Boott in W. J. Hooker		b; na	1	ca, m, d	—
29	*Rupestres* (Tuck.) Meinsh.	*rupestris* All.		aa; cp	2	ca, m, d	—
30	*Lamprochlaenae* (Drejer) L. H. Bailey in J. M. Coulter	*glacialis* Mack.		aa; cp	2	d	—
		supina Willd. ex Wahlenb.	subsp. *spaniocarpa* (Steud.) Hultén	a; na-ea	2	m, d	—
31	*Leptocephalae* L. H. Bailey	*leptalea* Wahlenb.	subsp. *leptalea*	b; na	2	w, s	—
32	*Nardinae* (Tuck.) Mack. in N. L. Britton et al.	*nardina* Fries		aa; amp	2	d	—
33	*Capituligerae* Kük.	*capitata* L.		aa*; cp	2	d	sc

[1] a = arctic; aa = arctic-alpine; b = boreal; hb = high boreal; la = low arctic; t = temperate; * = bipolar; amp = amphi-Atlantic; cb = circumboreal; cbd = circumboreal disjunct; co = cordilleran; cp = circumpolar; cpd = circumpolar disjunct; na = North American; na-ea = North American and East Asian; nea = northeastern American; nea-ea = northeastern American and East Asian.

[2] 1 = rare, 12 sites or less; 2 = moderately common; 3 = very common and widespread.

[3] c = coastal; ca = obligate calcicolous; d = dry; m = mesic; mb = mud boils; s = shores; sb = snow beds; w = wetlands, including peatlands and salt marshes.

[4] h = hybrid; iv = infraspecific variation; sc = species complex.

APPENDIX 2

Specimens of *Carex lapponica* and *C.* ×*flavicans* cited in Figures 4A and 5A.

Carex lapponica in northeastern North America (Fig. 4A):

MANITOBA. Big Spruce River, 10 miles upstream from junction with Seal River, in wet peat with *Sphagnum* of black spruce muskeg, 23 July 1956, *J. C. Ritchie 2040* (CAN, DAO, MT); Churchill, found fairly commonly in peaty swamps of this region, alt. 30–50 ft., 26 July 1957, *E. Beckett 86* (BM) [sub *C. mackenziei*; but the LKHD duplicate is *C. mackenziei*]; Little Duck Lake, wet shore meadow, 10 July 1974, *D. Punter s.n.* (DAO, LKHD). QUEBEC. Nunavik, Fort Chimo area [Kuujjuaq], between Inukshuktujuk and Ft. Chimo, grid 427717, 58°23′N–68°18′W, alt. 300 ft., 28 July 1967, *Y. Mäkinen 67-1245* (CAN); idem, 58°07′N–68°23′W, moist depression in tundra area, 2 Aug. 1948, *J. Calder 2315* (S) (Toivonen, 1981a) [the corresponding duplicate in DAO is *C. canescens* subsp. *canescens*]; région du lac Chavigny, secteur sud-est, 58°03′N–75°05′W, en bordure d'un lac marécageux, dans les mousses très humides, avec *Galium trifidum*, 28 July 1982, *J. Cayouette J82-191* (DAO, MICH, MT, QFA); idem, avec *Carex aquatilis*, *C. rotundata*, *Eriophorum angustifolium*, 5 Aug. 1982, *J. Cayouette J82-303* (DAO, QFA); Povungnituk, ca. 60°21′N–77°15′W, nord-est du village, bord de mare tourbeuse, avec d'autres *Carex* hydrophiles, 28 July 1969, *M. Bournérias 69211* (MTMG, QFA) [sub *C. canescens*].

Carex ×*flavicans* in Quebec-Labrador north of 54°N (Fig. 5A):

QUEBEC. Hudson Bay, détroit des Manitounuk, fond d'une baie, haut rivage, herbaçaie basse dominée par *Carex subspathacea* et quelques arbustes, 55°39′45″N–77°07′00″W, 10 July 1981, *J. Cayouette & P. Dumas J81-231* (DAO, GH, MICH, MT, QFA, TRT); idem, haut rivage du détroit, non envahi par les marées, arbustaie rampante très humide, avec *Salix candida*, *Carex rariflora*, *Primula egaliksensis*, *Triglochin maritimum*, *Pedicularis sudetica*, etc., 10 July 1981, *J. Cayouette & P. Dumas J81-264* (DAO, QFA); idem, marais côtier, 55°37′N–77°12′W, 14 Aug. 1985, *J. Deshaye 90-868* (QFBE); Golfe de Richmond, hydrolittoral saumâtre, 1971–1973, *S. Payette et al. GR-107* (QFA) [sub *C. salina*]; Akulivik, marais côtier, avec *Hippuris vulgaris* et *Carex subspathacea*, 60°48′N–78°12′W, 22 Aug. 1985, *S. Dupuis AK-19* (QFA) [sub *C. salina*]; Ungava Bay, Kangiqsualujjuaq, estuaire de la rivière George, rivage de la baie au nord-est du village; au-delà de la limite supérieure de la prairie saumâtre, butte couverte de *Betula glandulosa*, *Empetrum* et *Vaccinium vitis-idaea* à sous-étage de lichens, 58°41′30″N–65°57′10″W, 19 July 1984, *Y. Pelletier & R. Gauthier 104* (QFA); Hudson Strait, Wakeham Bay [61°36′N–71°58′W], 29–30 July 1936, *N. Polunin 1432* (CAN, OXF) [sub *C. salina*].

Chapter 8

Allozyme Variation in the Genus *Carex*... 15 Years Later: 1986–2001

Leo P. Bruederle, Stephen L. Yarbrough, and Shannon D. Fehlberg

ABSTRACT A large body of population genetic data has accumulated for *Carex* L. (Cyperaceae) that provides a valuable foundation for systematic and evolutionary research on the genus. Since 1986, allozyme analysis has been conducted on more than 50 species representing 15 sections. In this paper, we summarize this literature and provide insight into the utility of these data to address hypotheses related to the evolution of *Carex* and graminoids in general. For example, in 1950, G. Ledyard Stebbins reported a relationship between growth form and breeding system among perennial grasses, with rhizomatous species predominantly outcrossing due to self-incompatibility and the intermingling of genets, while inbreeding was demonstrated for self-compatible caespitose "bunch-grasses." A summary based upon data for *Carex* supports this hypothesis. In comparison to caespitose species, rhizomatous carices average nearly three times as many polymorphic loci and more than four times as much expected heterozygosity as would be expected for outcrossing species. Furthermore, populations of caespitose carices often exhibit reductions in heterozygosity and significantly greater genetic differentiation than those of rhizomatous species. The effect of dioecy on population genetic structure is explored using the dioecious *C. scirpoidea* Michx. Although high levels of genetic diversity were expected, overall levels were moderate to low based on data collected for 17 loci from a sample of five Colorado populations. As expected for obligate outcrossers, genetic diversity was apportioned predominantly within populations, with a trend toward heterozygote excess. Only 12.3% of genetic diversity is attributable to differences among populations.

KEY WORDS Allozyme variation, *Carex*, Cyperaceae, population genetics.

Since the first publication describing allozyme variation in the genus *Carex* L. and the utility of these data for systematic purposes (i.e., Bruederle & Fairbrothers, 1986), there have been more than 30 publications and several unpublished studies that have applied allozyme analysis to the study of the systematics and evolution of this species-rich genus (Table 1). There are very few other plant genera, e.g., *Pinus* L. (Pinaceae), for which such a large body of population genetic data has accumulated for so many different congeners (Ledig, 1998). Whereas reviews summarizing the population genetic literature exist for plants, in general (e.g., Hamrick & Godt, 1990), none has been compiled for *Carex*.

While there is a variety of molecular techniques by which to obtain population genetic data, the majority of the data summarized herein derive from allozyme analysis. This approach utilizes electrophoresis to separate differentially charged, enzymatic proteins. Following electrophoresis, substrate-specific stains reveal the allelic forms of enzymes (i.e., allozymes), from which individual genotypes are extrapolated and subjected to various population genetic analyses (see Soltis & Soltis, 1989). Although the advantages and disadvantages of allozyme analysis have been thoroughly discussed in the literature (e.g., Lee et al., 2002), the great advantage of allozyme markers is their Mendelian inheritance and genetic co-dominance, allowing for the ready identification of heterozygous individuals (cf., morphology, random applications of polymorphic DNA [RAPDs], amplified fragment length polymorphisms [AFLPs]). Furthermore, an extensive literature discussing allozyme variation in *Carex* has been accumulated since 1986, providing a notable frame of reference for research being undertaken on carices, both with respect to experimental design (field techniques, laboratory techniques, and statistical analyses) and the interpretation of results.

Within the genus *Carex*, allozyme data have been used for a variety of purposes. Systematists have used these data to determine the extent of genetic differentiation and, coupled with cytological, morphological, or ecological data, to ascertain taxonomic rank, e.g., *C. mitchelliana* M. A. Curtis (Bruederle, 1999); elucidate systematic relationships among taxa, both within species complexes, e.g., *C. timida* Naczi & B. A. Ford in the *C. jamesii* Schwein. complex (Ford & Naczi, 2001), and within sections of the genus, e.g., *Carex* section *Phyllostachyae* Tuck. ex Kük. (Ford et al., 1998c); and test hypotheses of hybrid origin, e.g., *C.* ×*knieskernii* Dewey (Waterway, 1994). These data have also been used to provide insight into evolution, e.g., *Carex* sect. *Phyllostachyae* (Ford et al., 1998b), and the role of recent historical factors such as Pleistocene glaciation, e.g., *C. rariflora* (Wahlenb.) Sm. (Vellend & Waterway, 1999); provide indirect estimates of mating systems, e.g., *C. crinita* Lam. complex (Bruederle & Fairbrothers, 1986); and reveal correlations between genetic diversity and structure, with respect to certain life-history traits, e.g., *C. humilis* Leyss. (Huh, 2001), including distribution, e.g., *C. hirtissima* W. Boott (Waterway, 1996).

Since 1986, more than 50 *Carex* species have been examined for allozyme variation, which, given the size of this genus estimated at 2000(–2500) species, comprises approximately 2% of described carices. Furthermore, a total of only 15 sections of the genus are represented in the literature summarized herein (see Table 1).

Nearly worldwide in distribution, *Carex* is best represented throughout the Northern Hemisphere, particularly in eastern Asia and North America (Ball & Reznicek, 2002). However, most research to date has considered taxa restricted to North America (e.g., *C. misera* Buckley; see Schell & Waterway, 1992) or North American populations of more widely distributed taxa (e.g., *C. viridula* Michx.; see Kuchel & Bruederle, 2000). Few taxa have been as thoroughly sampled geographically as *C. arenaria* L. in western Europe (Jonsson & Prentice, 2000). Eurasian and Asian taxa, in particular, have received considerably less attention, with no taxa restricted in distribution to the Southern Hemisphere having yet been studied. The ecological amplitude of the genus has not been fully considered either. For example, while the sedges comprising this genus occur across a wide elevational gradient and are commonly encountered at high elevations, surprisingly few alpine species have been examined; exceptions include *C. arctogena* Harry Sm. (Reinhammar, 1999). Finally, much of the variation exhibited by *Carex* for life-history traits, e.g., seed dispersal, as well as other aspects of its biology, has yet to be explored.

Regardless, this body of data is impressive and nearly unparalleled among plants. As this literature

has not been summarized previously in its entirety (see Vellend & Waterway, 1999; Jonsson & Prentice, 2000; Huh, 2001), we take the opportunity to do so here. As such, this chapter represents an attempt to summarize this literature and, while far from complete, provides insight into the utility of these data for addressing hypotheses important not only to the complex evolution of *Carex*, but all plants. First, the potential for identifying trends within the data set will be discussed, exemplified by testing a hypothesis regarding the correlation of breeding systems with habit first proposed for grasses (Stebbins, 1950). Second, the utility of these data for comparative purposes will be discussed, wherein we will compare population genetic structure in a dioecious species, *C. scirpoidea* Michx., with that in monoecious carices. Concluding statements will address future directions, including cautionary statements.

Trends and Generalizations: Growth Habit and Breeding System

It has become clear that the amount of genetic diversity maintained within and among populations of different plants is influenced by each species' life history, geographic and ecological distribution, and recent evolutionary history. Summarizing the plant population genetic literature, Hamrick and Godt (e.g., 1990) reported statistically significant correlations for a variety of life-history parameters (e.g., mode of dispersal and perennation) despite considerable variation within their data set, both with respect to experimental design and the genotypic data analyzed. We can similarly expect to find patterns within the allozyme data set for *Carex*. One such pattern, with respect to breeding system, has already received considerable attention—notable discussions of the role that growth form, and other factors, may play with respect to the levels and apportionment of genetic diversity include Ford et al. (1991, 1998a), Jonsson and Prentice (2000), and Huh (2001).

In 1950, G. Ledyard Stebbins postulated a relationship between growth form and breeding system based on a sample of 71 perennial species representing seven genera of grasses. Rhizomatous species were predominantly outcrossing due to self-incompatibility and the intermingling of genets (genetically distinct individuals) as a consequence of spreading growth involving rhizomes. In contrast, inbreeding was predominant among self-compatible caespitose species, for which intermingling of genets was expected to be less likely. Genetic evidence substantiating the latter in *Carex* (Cyperaceae) was first reported by Bruederle (1987) from divergent members within *Carex* sect. *Phacocystis* Dumort. Since then, numerous population genetic studies have been conducted on both caespitose and rhizomatous carices.

On average, carices tend to maintain less genetic diversity than reported for all plants by Hamrick and Godt (1990). For *Carex* (N = 45), an average of 24.9 ± 18.5% of a populations' loci are polymorphic (P), with an average number of alleles per polymorphic locus (A_P) of 2.1 ± 0.1. Furthermore, mean expected heterozygosity (H_e) is 0.085 ± 0.086, with population differentiation (G_{ST}) averaging 34.4 ± 25.8% (Table 2). However, it is apparent from the range and large standard deviations that these summary statistics may be complicated by any of a number of factors, among them differences in growth form and breeding system.

Kuchel and Bruederle (2000) conducted a survey of the literature, which included allozyme data for 29 carices; among these were six rhizomatous and 23 caespitose taxa. On average, populations of rhizomatous species were found to harbor relatively high levels of genetic diversity (e.g., P = 44.5 ± 4.1%, A_P = 2.3 ± 0.1, H_e = 0.171 ± 0.038) when compared to caespitose species, which maintained significantly less (e.g., P = 13.4 ± 12.0%, A_P = 2.0 ± 0.1, H_e = 0.042 ± 0.004). Yarbrough (2000) reported significant statistical differences ($p < 0.05$) between the aforementioned caespitose and rhizomatous carices for each of the aforementioned genetic diversity parameters using the Mann-Whitney U-test for nonparametric data. A summary based on all available data collected between 1986 and 2001 mirrors those results (Table 2); that is, the genetic diversity maintained by populations of rhizomatous species (i.e., P = 41.9 ± 12.9%, A_P = 2.2 ± 0.1, H_e = 0.180 ± 0.084) differs significantly ($p < 0.05$) from that for caespitose carices (i.e., P = 14.2 ± 12.4%, A_P = 2.1 ± 0.1, H_e = 0.043 ± 0.044). Rhizomatous species average nearly three times as many polymorphic loci and more than four times as much expected heterozygosity when compared to caespitose carices.

With respect to genetic structure, or the spatial apportionment of genetic diversity, populations of rhi-

Table 1. Summary of the allozyme literature, with respect to the genus *Carex* L. (Cyperaceae) including section represented, taxa sampled, and author(s) with year of publication.

Section	Taxon (including subspecies and variety)	Source
Acrocystis Dumort.	*C. montana* L.	Kay & John (1994)
Ammoglochin Dumort.	*C. arenaria* L.	Jonsson & Prentice (2000)
Capituligerae Kük.	*C. capitata* L. s. str.	Reinhammar (1999)
	C. arctogena Harry Sm.	
Ceratocystis Dumort.	*C. flava* L.	Bruederle & Jensen (1991)
	C. viridula Michx.	
	C. lepidocarpa Tausch s. str.	Hedren (1996)
	C. jemtlandica Palmgr.	
	C. lepidocarpa Tausch s. str.	Hedren & Prentice (1996)
	C. jemtlandica Palmgr.	
	C. viridula Michx.	Kuchel & Bruederle (2000)
Clandestinae G. Don	*C. humilis* Leyss. var. *nana* (H. Lév. & Vaniot) Ohwi	Huh (2001)
Hymenochlaenae (Drejer) L. H. Bailey	*C. gynodynama* Olney	Waterway (1990)
	C. mendocinensis Olney ex W. Boott	
	C. misera Buckley	Schell & Waterway (1992)
	C. ×*knieskernii* Dewey	Waterway (1994)
	C. arctata Boott	
	C. castanea Wahlenb.	
	C. hirtissima W. Boott	Waterway (1996)
	C. misera Buckley	Godt et al. (1996)
Hymenochlaenae	*C. hondoensis* Ohwi	Huh & Huh (1998)
Limosae (Heuff.) Meinsh.	*C. rariflora* (Wahlenb.) Sm.	Vellend & Waterway (1999)
Mitratae Kük.	*C. breviculmis* R. Br.	Huh et al. (2000)
Ovales Kunth	*C. preslii* Steud.	Whitkus (1992)
	C. macloviana d'Urv.	
	C. pachystachya Cham. ex Steud.	
	C. subfusca W. Boott.	
	C. integra Mack.	
	C. abrupta Mack.	
	C. harfordii Mack.	
	C. subbracteata Mack.	
Paludosae G. Don	*C. vestita* Willd.	Standley et al. (1991)
	C. lasiocarpa Ehrh.	McClintock & Waterway (1993)
	C. pellita Muhl. ex Willd.	
	C. lasiocarpa Ehrh.	McClintock & Waterway (1994)
	C. pellita Muhl. ex Willd.	
Paniceae G. Don	*C. polymorpha* Muhl.	Standley et al. (1991)
Phacocystis Dumort.	*C. crinita* Lam. var. *crinita*	Bruederle & Fairbrothers (1986)
	C. gynandra Schwein.	
	C. mitchelliana M. A. Curtis	
	C. bigelowii Torr. ex Schwein.	Jonsson et al. (1996)

Table 1. Continued.

Section	Taxon (including subspecies and variety)	Source
	C. mitchelliana M. A. Curtis	Bruederle (1999)
Phacocystis	*C. bigelowii* Torr. ex Schwein.	Stenström et al. (2001)
	C. ensifolia Turcz. subsp. *arctisibirica* Jurtsev	
	C. lugens T. Holm	
	C. stans Drejer	
Phyllostachyae Tuck. ex Kük.	*C. willdenowii* Schkuhr ex Willd.	Ford et al. (1998a)
	C. basiantha Steud.	
	C. superata Naczi, Reznicek & B. A. Ford	
	C. backii Boott	Ford et al. (1998b)
	C. basiantha Steud.	
	C. jamesii Schwein.	
	C. juniperorum Catling, Reznicek & Crins	
	C. latebracteata Waterf.	
	C. saximontana Mack.	
	C. superata Naczi, Reznicek & B. A. Ford	
	C. willdenowii Schkuhr ex Willd.	
	C. backii Boott	Ford et al. (1998c)
	C. basiantha Steud.	
	C. jamesii Schwein.	
	C. juniperorum Catling, Reznicek & Crins	
	C. latebracteata Waterf.	
	C. saximontana Mack.	
	C. superata Naczi, Reznicek & B. A. Ford	
	C. willdenowii Schkuhr ex Willd.	
	C. jamesii Schwein.	Ford & Naczi (2001)
	C. juniperorum Catling, Reznicek & Crins	
	C. timida Naczi & B. A. Ford	
Scirpinae (Tuck.) Kük.	*C. scirpoidea* Michx. subsp. *scirpoidea*	Yarbrough (2000)
Vesicariae (Heuff.) J. Carey	*C. saxatilis* L. complex (including *C. miliaris* Michx. and *C. physocarpa* C. Presl)	Ford et al. (1991)
	C. membranacea Hook.	
	C. rotundata Wahlenb.	
	C. saxatilis L.	Ford et al. (1993)
	C. membranacea Hook.	
	C. rotundata Wahlenb.	
	C. utriculata Boott	
	C. rostrata Stokes	
	C. vesicaria L.	
	C. ×*mainensis* Porter ex Britton = *C.* ×*stenolepis* Less.	
	C. ×*physocarpoides* Lepage	
	C. membranacea × *utriculata*	

Table 2. Summary statistics, including mean, standard deviation (SD), and range for 44 taxa[1] based on values reported in the allozyme literature between 1986 and 2001 for *Carex* L. (Cyperaceae), where P is the proportion of loci polymorphic, A_P is the number of alleles per polymorphic locus, H_e is expected heterozygosity, and G_{ST} is population differentiation.

	P(%)	A_P	H_e	G_{ST}(%)
All carices (N = 45 reports[1])				
Mean	24.9	2.1	0.085	34.4
SD	18.5	0.1	0.086	25.8
Range	0.0–75.0	2.0–2.7	0.000–0.337	0.0–96.7
Caespitose carices (N = 28)				
Mean	14.2	2.1	0.043	41.2
SD	12.4	0.1	0.044	27.6
Range	0.0–40.2	2.0–2.3	0.000–0.148	0.0–96.7
Rhizomatous carices (N = 17)				
Mean	41.9	2.2	0.180	22.8
SD	12.9	0.1	0.084	17.9
Range	19.0–75.0	2.1–2.4	0.056–0.337	2.5–55.3

[1] There are two reports for *C. misera* (Schell & Waterway, 1992; Godt et al., 1996).

zomatous species typically meet Hardy-Weinberg expectations, while populations of caespitose carices often exhibit statistically significant heterozygote deficiency as indicated by positive fixation indices (F); values for this statistic may range from –1 to 1, with positive values indicating a reduction in heterozygosity due to inbreeding. Whereas populations of rhizomatous species are poorly differentiated (G_{ST} = 15.9 ± 5.3%), those of caespitose carices are typically well differentiated, with nearly half of all genetic diversity attributable to differences among populations (G_{ST} = 46.2 ± 27.2), this difference again being statistically significant ($p < 0.05$) using the Mann-Whitney U-test for nonparametric data assuming that values reported for G_{ST} and F_{ST} estimate the same parameter (Kuchel & Bruederle, 2000; Yarbrough, 2000). Summarizing the literature published between 1986 and 2001, the pattern remains—populations of caespitose carices exhibit greater genetic differentiation (G_{ST} = 41.2 ± 27.6%) than those of rhizomatous species (G_{ST} = 22.8 ± 17.9%), despite differences in sampling strategies on which this statistic is dependent (e.g., sampling range).

Factors in addition to the genet intermingling proposed by Stebbins (1950) undoubtedly contribute to the increased diversity reported for most rhizomatous species. Notable among these is the organization of the inflorescence, with respect to the proximity, composition, and phenology of spikelets (Ford et al., 1991, 1998a). Although crossing studies in *Carex* are few, most species for which these data are available have been shown to be self-compatible (Whitkus, 1988). Demographic factors, including sexual recruitment with seedling establishment and subsequent asexual reproduction, assuming clonal longevity, are expected to increase genetic diversity within populations of rhizomatous species, as well (Huh, 2001), although decreases in genetic variation correlated with successional status have been reported by McClintock and Waterway (1993).

Clearly the phenomenon proposed by Stebbins for grasses is evident for many carices, at least with certain caveats. Deviations, including the elevated diversity and reduced population differentiation that have been reported for some caespitose carices, e.g., *Carex willdenowii* Schkuhr ex Willd., may be attributable to other ecological and evolutionary forces, e.g., selection and differential seed dispersal (Ford et al., 1998a). Similarly, levels of diversity reduced from expectations may be attributable to recent historical factors, e.g., post-glacial migration, as sug-

gested by Jonsson and Prentice (2000) for populations of the rhizomatous *C. arenaria*. Additionally, this discussion has not taken into consideration variations in the design of research, including sampling, data collection, and statistical analyses. Nor does it consider the complex nature of habit (Jermy et al., 1982) and variation in mating systems and sexual systems (e.g., dioecy) that occurs in *Carex*, all of which can affect these descriptive statistics and our interpretations of data.

Carex scirpoidea: A Case Study for Comparing Dioecious and Monoecious Carices

Carex scirpoidea subsp. *scirpoidea* (section *Scirpinae* (Tuck.) Kük.) is a dioecious, loosely caespitose/short rhizomatous taxon. It is generally widespread and continuously distributed across the northern latitudes of North America, from the arctic and subarctic, south through the New England states and much of western Canada. It also occurs in several disjunct pockets in the Great Lakes region and throughout the Rocky Mountains of the western United States. Colorado populations of *C. scirpoidea* subsp. *scirpoidea* principally occupy peaty hummocks at the edges of rich to extremely rich fens in the upper montane through lower alpine life zones.

Yarbrough (2000) considered the effect of dioecy on population genetic structure using *C. scirpoidea* subsp. *scirpoidea* as a model system. Although other authors, e.g., Jelinski and Cheliak (1992), have previously considered the effect of dioecy on population genetic structure, many of these studies have been complicated by the varying forms of dioecy being evaluated (i.e., strict dioecy, gynodioecy, androdioecy, subdioecy, and cryptic dioecy). Therefore, while the effect of strict dioecy is theoretically predictable, in practice it has been difficult to generalize with respect to the impact of this sexual system.

The majority of the data describing population genetic diversity and structure in *Carex* has considered monoecious species, the dominant sexual system, in which each individual plant bears unisexual male and unisexual female flowers variously organized into spikes. Dioecy is uncommon in *Carex*, occurring in only a few divergent sections (Martens, 1939), with the effect of dioecy not having been previously addressed. Dunlop (1990) found members of *Carex* sect. *Scirpinae* to be strictly dioecious, resulting in obligate outcrossing. As such, Yarbrough (2000) presumed high levels of genetic diversity that, despite its caespitose habit, would be apportioned within, rather than among, populations of *C. scirpoidea* subsp. *scirpoidea*.

Yarbrough (2000) sampled five populations of *Carex scirpoidea* subsp. *scirpoidea* from wetlands located in Park County, Colorado. Soluble enzymatic proteins were extracted from leaf tissue harvested from a minimum of 50 plants per population, with roughly equal numbers of male and female plants collected. Sex expression in *C. scirpoidea* is fixed, with the ratio of male to female plants approximately 1:1 in most populations (Dunlop, 1990). Methods and materials for allozyme extraction and starch gel electrophoresis followed Bruederle and Fairbrothers (1986) and Bruederle and Jensen (1991), with data collected for 17 putative loci (Yarbrough, 2000). Statistical analyses were performed on genotypic data at both the species and population level to obtain means and standard error values for standard measures of genetic diversity, following Hamrick and Godt (1990). Chi-square tests were used to evaluate deviations from Hardy-Weinberg equilibrium, with fixation indices (F) calculated for each polymorphic locus. Summary F- and G-statistics were calculated to determine the apportionment of genetic diversity within and among populations. All population genetics statistics were calculated using BIOSYS-1 (Swofford & Selander, 1981) and GENESTAT-PC software (Lewis & Whitkus, 1989).

Overall levels of genetic diversity within populations of *C. scirpoidea* subsp. *scirpoidea* were found to be moderate to low when compared to other plants for which these data have been summarized. Percentage of loci polymorphic (0.05 criterion) ranged from 11.8% to 29.4%, with an overall population mean of 20.0 ± 6.7%. Average number of alleles per locus (A) varied from 1.2 to 1.4, with a mean value of 1.3 ± 0.1. The mean value for average number of alleles per polymorphic locus (A_P) was 2.2 ± 0.1. Species-level statistics revealed that 29.4% of loci were polymorphic in *C. scirpoidea* subsp. *scirpoidea*. Similarly, species-level values for A (1.5) and A_P (2.3) were also larger than population-level statistics.

Mean observed heterozygosity across populations (H_o) was 0.074 ± 0.028 or 7.4%, while mean

expected heterozygosity per locus (H_e) ranged from 0.051 to 0.092, with an overall mean of 0.068 ± 0.019 or approximately 7%. Expected heterozygosity at the species level (H_T) was 0.078 or approximately 8%. These three values are very similar, deviating by no more than 1%, thus suggesting that these populations are panmictic or randomly breeding, meeting Hardy-Weinberg expectations. However, chi-square tests (χ^2) revealed 15 significant deviations ($p < 0.05$) from Hardy-Weinberg expectations for five polymorphic loci across all five populations, with a trend toward heterozygote excess as revealed by small, negative fixation indices. Summary *F*-statistics for *Carex scirpoidea* subsp. *scirpoidea* similarly revealed a tendency from random mating in the direction of expectations for obligate outcrossing at five of seven polymorphic loci ($F_{IS} = -0.097$).

As anticipated for obligate outcrossers, genetic diversity is apportioned predominantly within populations of *Carex scirpoidea* subsp. *scirpoidea*. Only 12.3% of the diversity found in these populations is attributable to differences among populations ($G_{ST} = 0.123$). That is, approximately 88% of genetic diversity is due to differences among individuals within populations of this dioecious sedge. These values are less than that for monoecious carices ($G_{ST} = 38.9\%$), and even other dioecious species ($G_{ST} = 20.4\%$). Population genetic structure in *C. scirpoidea* subsp. *scirpoidea* reveals a pattern similar to rhizomatous carices ($G_{ST} = 15.9\%$), with genetic diversity apportioned within rather than among populations (Kuchel & Bruederle, 2000). Not surprisingly, dioecy imparts obligate outcrossing and promotes the gene flow that prevents these populations from experiencing the effects of inbreeding typical of many other caespitose carices. Dioecy in this sense may be a stabilizing force helping to maintain genetic diversity in populations of *C. scirpoidea* subsp. *scirpoidea*.

As previously noted, comparisons among carices may be confounded by growth form. In order to evaluate this phenomenon, comparisons of genetic diversity were made between caespitose and rhizomatous carices, all of which are monoecious, and the strictly dioecious *Carex scirpoidea* subsp. *scirpoidea*. Colorado populations of *C. scirpoidea* subsp. *scirpoidea* maintained a greater proportion of polymorphic loci (20%) than caespitose carices (14%), but substantially fewer polymorphic loci than rhizomatous carices (44%). *Carex scirpoidea* subsp. *scirpoidea* populations averaged 1.3 alleles per locus, versus 1.2 for caespitose carices and 1.6 for rhizomatous carices. Observed heterozygosity was more than twice as high in *C. scirpoidea* subsp. *scirpoidea* (7.4%) relative to other caespitose carices (3.3%), but substantially less than rhizomatous carices (17.4%). Mann-Whitney *U*-tests found *C. scirpoidea* subsp. *scirpoidea* populations to be significantly different ($p < 0.05$) in terms of genetic diversity compared to both caespitose and rhizomatous carices.

Low levels of genetic diversity in Colorado populations of *Carex scirpoidea* subsp. *scirpoidea* were unexpected and may be attributable to several factors, including recent evolutionary history, disjunct distribution, and substrate-specificity. Although no population data are available from more northern latitudes of North America, it is reasonable to assume that genetic diversity in the biogeographic center for the species is greater than that found in Colorado populations, which are disjunct by 1100 km (Bruederle, 1999). Furthermore, Colorado populations of *C. scirpoidea* subsp. *scirpoidea* seemingly maintain a narrow tolerance for substrate, occurring almost exclusively in fens high in calcium and magnesium, severely limiting expansion of this species. As such, reduced gene flow, random genetic drift, and natural selection are expected to result in levels of genetic diversity that are lower than might be expected for a dioecious species.

Compared to a summary of the plant population genetic literature compiled by Hamrick and Godt (1990), it is clear that Colorado populations of *Carex scirpoidea* subsp. *scirpoidea* harbor less genetic diversity than that found in an average plant population ($P_{0.05} = 34.2\%$, $A = 1.5$; $H_e = 11.3\%$). Similarly, Mann-Whitney *U*-tests revealed *C. scirpoidea* subsp. *scirpoidea* populations to differ significantly ($p < 0.05$) for the parameters *P*, *A*, H_o, and H_e compared with other dioecious flowering plants, for which these data are available. However, no significant differences ($p > 0.05$) were found between *C. scirpoidea* subsp. *scirpoidea* and monoecious carices for any of the genetic diversity parameters tested.

Conclusions

There exists for *Carex* a large and rich body of allozyme data that has yet to be thoroughly mined. These data provide an important frame of reference

for research on carices, with respect to testing evolutionary hypotheses. Furthermore, utilizing phylogenies that are being developed for the genus will allow caricologists to make "cladistic comparisons" (Stebbins, 1988), testing evolutionary hypotheses within a phylogenetic framework.

While this discussion has not taken into consideration the impact of variations in the design of research, which include sampling (e.g., number of populations sampled, distribution of populations sampled, and number of individuals sampled), data collection (e.g., enzyme systems assayed and loci sampled), and statistical analyses (e.g., ramet vs. genet and statistical rigor), it will be important for future research to do so. Recognizing the complexity of most life-history traits, thoughtful experimental design, and careful statistical analysis can provide insights into the evolutionary biology of this group afforded few others.

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Chapter 9

Phylogeny and Patterns of Convergence in *Carex* Sect. *Ovales* (Cyperaceae): Evidence from ITS and 5.8S Sequences

Andrew L. Hipp

ABSTRACT *Carex* L. sect. *Ovales* Kunth, with approximately 85 species worldwide, is one of the largest sections in the genus and the largest in *Carex* subg. *Vignea* (P. Beauv. ex T. Lestib.) Peterm. (ca. 400 species). Sequence data from the internal transcribed spacer (ITS) region and 5.8S gene of nuclear ribosomal DNA (nrDNA) demonstrate that section *Ovales* is monophyletic, including the East Asian *C. maackii* Maxim. and the two species of section *Cyperoideae* G. Don, but excluding *C. illota* L. H. Bailey. The two main synapomorphies that define section *Ovales*—winged perigynia and true vegetative culms—have each evolved independently in at least one other lineage in the genus. Moreover, the traditional infrasectional taxonomy of section *Ovales* is based on morphological characters that are for the most part homoplastic. The majority of eastern North American species in section *Ovales* form a single lineage ("ENA Clade I") that derives from a poorly resolved western North American group.

KEY WORDS *Carex*, Cyperaceae, ITS phylogeny, nrDNA, section *Cyperoideae*, section *Ovales*, subgenus *Vignea*.

Section *Ovales* Kunth is one of the largest sections in *Carex* L. subg. *Vignea* (P. Beauv. ex T. Lestib.) Peterm. The section contains 72 North American species (Mastrogiuseppe et al., 2002), 10 additional species of South and Central America, and three species that are confined to the Old World, for a total of ca. 85 species worldwide (Reznicek, 1993; Mastrogiuseppe et al., 2002). The section ranges from floodplain forests to alpine tundra, encompassing much of the ecological diversity of the entire genus (Wheeler & Ownbey, 1984; Hipp, 1998). Regionally endemic species complexes account for much of the section's diversity and raise the question of whether speciation rate is elevated within section *Ovales* (Hermann, 1970; Raven & Axelrod, 1978; Whitkus & Packer, 1984; Whitkus, 1988; Reznicek & Rothrock, 1997; Rothrock & Reznicek, 2001).

Section *Ovales* is distinguished by the presence of winged perigynia borne in gynecandrous spikes, a caespitose growth form with very short rhizomes in all but a few species, and true vegetative culms, which may become elongate and root at the nodes late in the season (Reznicek & Catling, 1986; Reznicek, 1993). This combination of characters makes the section easily recognizable even if distinguishing species poses difficulties. Mackenzie (1935) recognized 11 informally named species groups within section *Ovales* based on characters of the perigynia, pistillate scales, leaf sheaths, and vegetative culms. Although a few of these species groups have strong ecological, geographical, and morphological homogeneity (e.g., the Tribuloideae and Alatae), Mackenzie's species groups are generally considered to be unnatural (Reznicek, 1993).

Two issues stand out regarding the circumscription of section *Ovales*. The first is the status of section *Cyperoideae* G. Don [= *Schellhammeria* (Moench) Kunth]. While the two species of section *Cyperoideae* sensu Tuckerman possess winged perigynia and gynecandrous spikes, their extremely elongate perigynia and unique inflorescence structure (Fig. 1) make them highly distinctive relative to the other members of section *Ovales*. Consequently, treatments in *Flora Europaea* (Chater, 1980), *The Sedges* (Carex *L.*) *of Russia and Adjacent States* (Egorova, 1999), and the *Flora of North America* (Mastrogiuseppe et al., 2002) treat the *Cyperoideae* as a separate section. Mackenzie (1935), however, recognized section *Cyperoideae* as a species group within *Ovales*. Many North American taxonomists follow Mackenzie's lead on this (e.g., Hermann, 1970; Gleason & Cronquist, 1991).

The second issue is the position of *Carex illota* L. H. Bailey, a gynecandrous species with unwinged perigynia that Kükenthal (1909) placed into section *Elongatae* Kunth. This section has subsequently been divided into sections *Deweyanae* Tuck., *Stellulatae* Kunth, and *Heleonastes* Kunth (in part), and *C. illota* might be expected to fall most naturally among one of those sections (Whitkus, 1988). Mackenzie (1935: p. 131), however, argued of *C. illota* that "its true relationship seems to be with the *Ovales*, of which it may be regarded as one of the most primitive species." The issue has not been addressed formally since Mackenzie.

While subgenus *Vignea* is known to be monophyletic (Reznicek, 1990; Starr et al., 1999, 2004, 2008; Yen & Olmstead, 2000; Roalson et al., 2001), relationships between and within most of its sections, including *Ovales*, have been examined in detail using molecular data by only a few workers (e.g., Hendrichs et al., 2004). This study uses sequence data from the internal transcribed spacer regions (ITS 1 and ITS 2) and the 5.8S gene of nuclear ribosomal DNA (nrDNA) to address the circumscription of section *Ovales*, the position of section *Ovales* within subgenus *Vignea*, and homoplasy in the characters that define section *Ovales* and the species groups that Mackenzie recognized within it.

Materials and Methods

Taxon Sampling

Subgenus *Vignea* outside of section *Ovales* was represented by 28 species from 15 sections (Table 1), including all species known to produce true vegetative culms (*Carex sartwellii* Dewey, *C. chordorrhiza* Ehrh. ex L. f., *C. pseudocuraica* F. Schmidt, along with the species of section *Ovales*) as well as species outside of section *Ovales* with obviously winged perigynia (*C. planata* Franch. & Sav., *C. brizoides* L., and *C. siccata* Dewey). Efforts to amplify *C. inversa* R. Br. of section *Inversae* Kük. and *C. curvula* All. of section *Curvulae* Tuck. were unsuccessful. Three outgroups were included from subgenus *Carex* and one from subgenus *Psyllophora* (Degl.) Peterm. [= *Primocarex* Kük.] based on their placement in prior studies (Roalson et al., 2001; Starr et

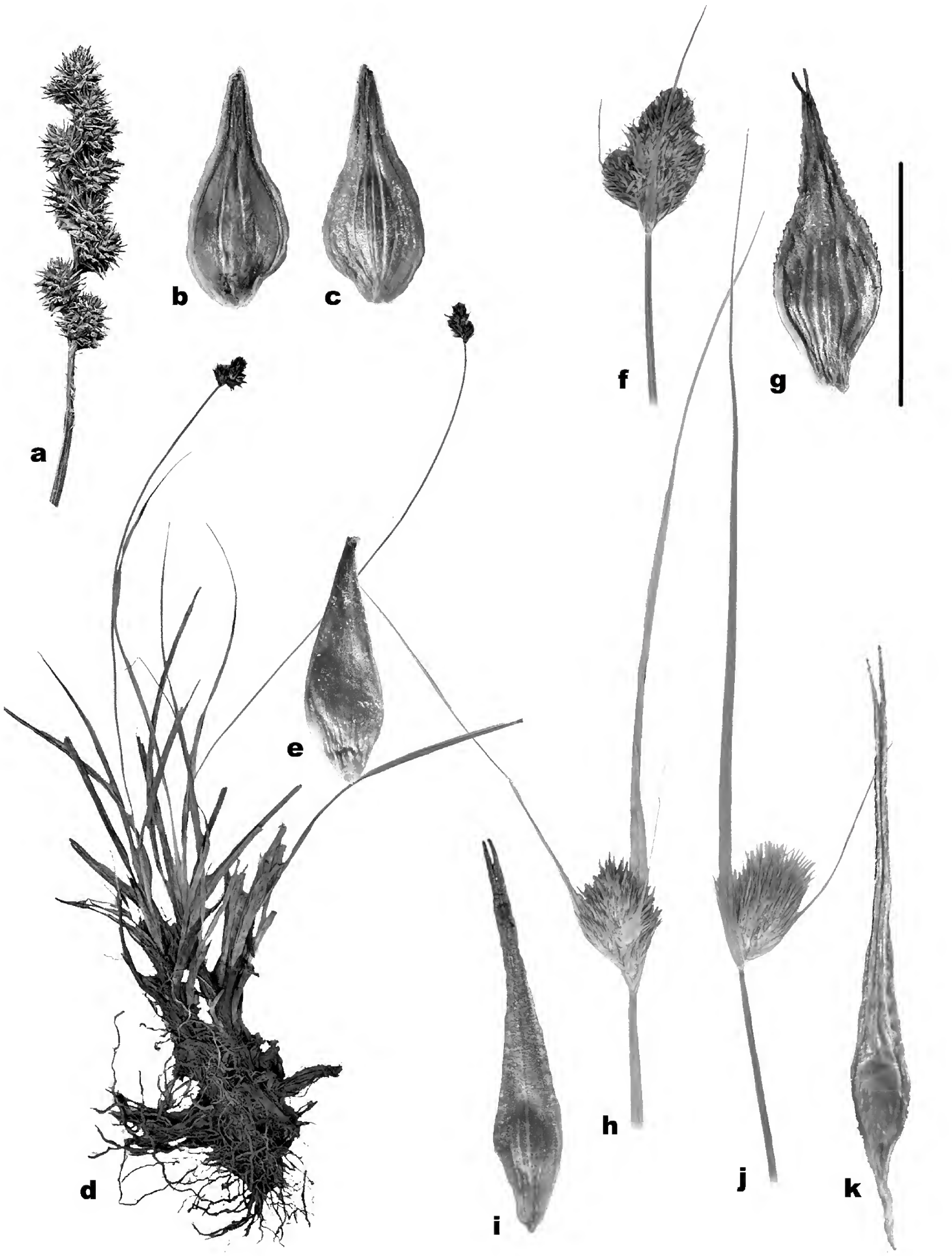

Figure 1. Inflorescences and perigynia of selected species. *Carex maackii*: —a. Inflorescence. —b. Perigynium, ventral face. —c. Perigynium, dorsal face (*Kan 8031*). *C. illota*: —d. Habit. —e. Perigynium, ventral face (*Hipp 700*). *C. athrostachya*: —f. Inflorescence (*Hipp 794*). —g. Perigynium (*Goodrich 22,204*). *C. sychnocephala*: —h. Inflorescence (*Iltis 13,453*). —i. Perigynium, ventral face (*Wedemeyer 135*). *C. bohemica*: —j. Inflorescence. —k. Perigynium, ventral face (*Wallnoffer 13755*). Scale bar = 3 mm (perigynia only; inflorescences not to scale).

al., 2004). Ninety accessions sampled from section *Ovales* represent 79 of the ca. 85 species recognized in the section. The placement of *C. chordorrhiza*, *C. illota*, and 29 other species was confirmed using sequences from two or more individuals of each species (Table 1). All sequences except for vulpinoidea1294, macrorrhiza, macrocephala, and ovalis24872 were generated for this study and are deposited in GenBank (numbers AY779064 to AY779182).

DNA EXTRACTION, POLYMERASE CHAIN REACTION, AND SEQUENCING

DNA was extracted from live, silica-dried, frozen, and herbarium tissue of single individuals using a modified 6× CTAB method (Doyle & Doyle, 1987) or DNEasy Plant Mini Kits (Qiagen, Valencia, California). The ITS region was amplified using the primers ITS-I (Urbatsch et al., 2000) and ITS-4 (White et al., 1990) in 50-µl reactions containing 5 µl $MgCl_2$ at 25 µM, 5 µl 10× $MgCl_2$-free *Taq* buffer, 0.5 µl 100× bovine serum albumin (BSA), 1.5 µl dimethyl sulfoxide (DMSO), 0.5 µl of each primer at 20 µM, 0.25 µl *Taq* DNA polymerase (1.25 units), and 29.75 µl ultrapure deionized water. Amplification was conducted in 30 polymerase chain reaction (PCR) cycles of DNA denaturation at 94°C for 30 seconds, primer annealing at 48°C for one minute, and extension at 72°C for one and a half minutes, ending with a single seven-minute extension at 72°C. Double-stranded PCR products were quantified on 0.8% ethidium bromide–stained agarose gels and cleaned using spin columns, QIAQuick (Qiagen, Valencia, California), or magnetic beads.

Cleaned PCR products were cycle-sequenced in half-reactions (10 µl) using BigDye reaction kits and the ITS-I and ITS-4 primers, with additional sequences using internal primers ITS-2 (White et al., 1990) and ITS-3B (Baum & Sytsma, 1994) for taxa in which ITS-I and ITS-4 sequences did not provide double coverage. Cycle sequencing products were precipitated in 75% ethanol or cleaned with magnetic beads and sequenced on Applied Biosystems (ABI) 377 or ABI 3100 automated sequencers at the University of Wisconsin–Madison Biotechnology Center's DNA Facility.

PHYLOGENETIC ANALYSIS

Sequences were edited and assembled in Sequencher 3.0 (GeneCodes Co., 1991–1995) and aligned manually in BioEdit 5.0.9 (Hall, 1999). Sequence alignments were unambiguous except for a few single base-pair indels. Alternate alignments at these points made no difference in topology or support for final trees. Indels were coded as present (1) or absent (0) and included in all parsimony analyses, which were performed in PAUP* 4.0b10 (Swofford, 1998). Heuristic parsimony searches were performed on equally weighted characters in 100 replicates of random sequence addition to detect multiple islands of most parsimonious (MP) trees (Maddison, 1991), with 1000 MP trees saved for each replicate (MULTREES = yes) and tree bisection-reconnection (TBR) branch swapping on all MP trees. Nonparametric bootstrap analysis (Felsenstein, 1985) was conducted using 500 heuristic bootstrap replicates of 100 random addition sequence replicates each, with one tree held at each step during stepwise addition (MULTREES = no) and TBR branch swapping (DeBry & Olmstead, 2000). Percent sequence divergence was calculated in PAUP* using the general time-reversible (GTR) model with other distance parameters at default settings.

Data were also analyzed using Metropolis-coupled Markov chain Monte Carlo (MCMC) in MrBayes v. 2.01 (Huelsenbeck & Ronquist, 2001). The GTR + I + G model was selected using a hierarchical likelihood ratio test of 24 sequence evolution models as implemented in MrModeltest 1.1b (Nylander, 2002). Prior probabilities were set at program defaults: topologies equiprobable; gamma distribution shape parameter uniform on the interval (0.05, 50.0); nucleotide frequencies and substitution rates uniform on the dirichlet distribution. Four parallel MCMC chains were run with heating parameter set at 0.2. Chains were run for 1,000,000 generations and trees sampled every 100 generations. Tree likelihood was graphed against generation number in Excel and the burn-in was visually determined to be confined to the initial 300,000 generations. Trees from these generations were eliminated prior to analysis. A second independent run was conducted to verify that trees were sampled from the correct distribution.

Monophyly of several sections and of species groups within section *Ovales* was tested using the Wilcoxon signed rank (WSR) test (Templeton, 1983) as implemented in PAUP*. Heuristic parsimony searches of 100 random addition replicates with TBR branch swapping on a single tree at each replicate were performed with the trees constrained to be monophyletic for each group in turn. Constrained MP trees were compared with an unconstrained MP tree for a total of 16 comparisons. One-tailed *P* values are reported and Bonferroni-corrected when significant (Buckley et al., 2001).

Results

ITS Data Matrix

The aligned ITS data matrix is 634 nucleotide positions in length, which includes all of ITS 1, 5.8S, and ITS 2, with the exclusion of the first three nucleotides at the 5′ end of ITS 1 for all taxa and 19 nucleotides at the 3′ end of ITS 2 in *Carex sartwellii* only. ITS 1 ranges from 216 to 222 nucleotides in length (excluding the first three nucleotides), ITS 2 from 219 to 227 nucleotides. One-hundred fifty-four nucleotide positions are parsimony-informative across the entire data set, 139 within subgenus *Vignea*, and 54 within section *Ovales* excluding *C. illota.* Maximum pairwise sequence divergence (GTR distances) among all taxa is 12.8%, 10.3% within subgenus *Vignea*, 4.1% within section *Ovales* excluding *C. illota.* Three single-nucleotide synapomorphies are found within the 5.8S region: a synapomorphy for the clade that includes section *Ovales* plus *C. illota* and *C. chordorrhiza*, a synapomorphy for *C. davyi* Mack. and *C. constanceana* Stacey, and a shared polymorphism between *C. planata* and *C. pensylvanica* Lam. Thirteen indels are potentially informative across all taxa included in this study, five within *Ovales.*

Phylogenetic Results

Heuristic searches of the combined data recovered 90,791 MP trees (Fig. 2). As this search was limited to swapping on 1000 trees at each random addition replicate, more MP trees are certain to exist. Addition of indels supports only one clade not recovered using nucleotide data alone: a clade composed of the core of Mackenzie's Tribuloideae (*Carex projecta* Mack., *C. tribuloides* Wahlenb., and *C. cristatella* Britton) plus *C. crawfordii* Fernald is supported by a single, homoplastic insertion that maps onto the tree with six or seven steps (depending on whether *C. cristatella* resolves with the other core Tribuloideae). The topology recovered in Bayesian analysis (Figs. 3 and 4) is slightly more resolved than the 50% majority rule consensus of MP trees (not shown) and significantly more resolved than the strict consensus (Fig. 2).

Monophyly of section *Ovales* with the exclusion of *Carex illota* is supported with posterior probability (PP) of 0.93 and parsimony bootstrap (PB) of 70%. *Carex chordorrhiza* and *C. pseudocuraica* form a strongly supported clade that is weakly supported as sister to section *Ovales* (PP = 0.75, PB = 44%). Within section *Ovales*, many small clades are recovered with moderate to weak support (Fig. 4). The largest clade recovered within the section is composed of the majority of eastern North American species in the section (eastern North America [ENA] Clade I; Figs. 2 and 4). The remainder of the tree is largely unresolved and composed of mostly western North American species. The East Asian *C. maackii* is resolved as sister to the rest of section *Ovales* (PP = 0.96, PB = 47%). The branch supporting this placement collapses in the strict consensus but is present in 97% of MP trees. The species of section *Cyperoideae* are embedded within section *Ovales*, but trees constrained such that sections *Ovales* and *Cyperoideae* are reciprocally monophyletic cannot be rejected (WSR test $P = 0.11$ before Bonferroni correction). Based on WSR test results, none of Mackenzie's named species groups are strongly rejected using ITS data alone.

Within the remainder of subgenus *Vignea*, two clades are supported with bootstrap support of 70% or higher (Fig. 3): one composed of section *Holarrhenae* (Doell.) Pax, the western North American *Phaestoglochin* Dumort. sampled, and the only member of section *Ammoglochin* Dumort. native to North America, and a second composed of the capitate eastern North American *Phaestoglochin* sampled, two sections with compound inflorescences (sections *Vulpinae* (Heuffel) Christ and *Multiflorae* (J. Carey) Kük.), and *C. vernacula* L. H. Bailey (section *Foetidae* (Tuck. ex L. H. Bailey) Kük.). Monophyly of section *Phaestoglochin* is strongly rejected (WSR $P < 0.0016$ with Bonferroni correction).

Table 1. Taxa included in study. Taxa for which two or more individuals were sequenced are marked with an asterisk (*). Sectional assignments follow Ball and Reznicek (2002) for most North American taxa, Egorova (1999) for most Old World taxa. Assignment to species group within section *Ovales* follows Mackenzie (1935) and Hermann (1970), with remaining species assigned according to morphology where feasible.

Carex species	Locality	Voucher	GenBank
Subgenus *Carex* L.			
Sect. *Acrocystis* Dumort.			
C. pensylvanica Lam.	U.S.A., Wisconsin	*Hipp 513* (WIS)	AY779137
Sect. *Hymenochlaenae* Drej. ex L. H. Bailey			
C. gracillima Schwein.	U.S.A., Wisconsin	*Hipp 505* (WIS)	AY779103
Sect. *Phacocystis* Dumort.			
C. haydenii Dewey	U.S.A., Wisconsin	*Hipp 501* (WIS)	AY779106
Subgenus *Psyllophora* (Degl.) Peterm. [= subg. *Primocarex* Kük.]			
Sect. *Capituligerae* Kük.			
**C. capitata* L.	U.S.A., Colorado	*Hipp & Hartman 1507* (WIS)	AY779079
Subgenus *Vignea* (P. Beauv. ex T. Lestib.) Peterm.—excluding sect. *Ovales*			
Sect. *Ammoglochin* Dumort.			
C. brizoides L.	Czechoslovakia	*Bohuslavek 694* (MICH)	AY779076
C. siccata Dewey	U.S.A., Wisconsin	*McNeilus 89-307* (WIS)	AY779158
Sect. *Chordorrhizae* Meinsh.			
**C. chordorrhiza* Ehrh. ex L. f.	U.S.A., Wisconsin	*Judziewicz 11790* (WIS)	AY779087
C. pseudocuraica F. Schmidt	China	*Lin 668* (MO)	AY779148
Sect. *Deweyanae* Tuck.			
**C. deweyana* Schwein. subsp. *deweyana*	U.S.A., Wisconsin	*DeJoode 1543* (WIS)	AY779094
Sect. *Divisae* Christ ex Kük.			
C. macrorrhiza Boeck.	Argentina, Santa Cruz	*Roivainen 2630* (RSA)	AF285018
C. praegracilis W. Boott	U.S.A., California	*Hipp 216* (WIS)	AY779143
Sect. *Foetidae* (Tuck. ex L. H. Bailey) Kük.			
**C. vernacula* L. H. Bailey	U.S.A., California	*Hipp & Clifton 680* (WIS)	AY779178

Sect. *Glareosae* G. Don			
**C. canescens* L.	U.S.A., Wisconsin	*Hipp et al. 587* (WIS)	AY779078
Sect. *Heleoglochin* Dumort.			
C. prairea Dewey ex A. W. Wood	U.S.A., Wisconsin	*Hipp & Zimmerman 602* (WIS)	AY779144
Sect. *Holarrhenae* (Doell.) Pax			
C. sartwellii Dewey	U.S.A., Wisconsin	*Hipp 515* (WIS)	AY779154
**C. curaica* Kunth	Russia, Siberia	*Krasnoborov et al. s.n.* (MO)	AY779092
Sect. *Macrocephalae* Kük.			
C. macrocephala Willd. ex Spreng.	U.S.A., Oregon	*Halse 1543* (RSA)	AF285017
Sect. *Multiflorae* (J. Carey) Kük.			
C. vulpinoidea Michx. (1)	U.S.A., Wisconsin	*Cochrane 13345* (WIS)	AY779180
C. vulpinoidea Michx. (2)	U.S.A., Texas	*Roalson 1294* (RSA)	AF284968
Sect. *Phaestoglochin* Dumort.			
C. cephaloidea (Dewey) Dewey	U.S.A., Wisconsin	*Hipp & Rothrock 1220* (WIS)	AY779080
C. cephalophora Muhl. ex Willd.	U.S.A., Wisconsin	*Hipp 528* (WIS)	AY779081
C. cf. *gravida* L. H. Bailey	U.S.A., Wisconsin	*Hipp 498* (WIS)	AY779083
C. hoodii Boott	U.S.A., California	*Hipp & Clifton 705* (WIS)	AY779107
C. muehlenbergii Schkuhr ex Willd.	U.S.A., Wisconsin	*Hipp 545* (WIS)	AY779124
C. occidentalis L. H. Bailey	U.S.A., New Mexico	*Hipp et al. 2067* (WIS)	AY779128
**C. radiata* (Wahlenb.) Small	U.S.A., Wisconsin	*Hipp 503* (WIS)	AY779149
C. rosea Schkuhr ex Willd.	U.S.A., Wisconsin	*Hipp 514* (WIS)	AY779153
Sect. *Potosinae* Mack.			
C. potosina Hemsl.	Mexico, Zacatecas	*Villegas & Garcia s.n.* (WIS)	AY779142
Sect. *Remotae* (Asch.) C. B. Clarke			
C. planata Franch. & Sav. (1)	Japan, Tarumizu	*Kurosawa 4025* (MO)	AY779140
C. planata Franch. & Sav. (2)	Japan, Honshu	*Tsugaru & Takahashi 26567* (MO)	AY779141
C. remota L.	former U.S.S.R.	*Novikov et al. 5863* (MO)	AY779150
Sect. *Stellulatae* Kunth			
C. interior L. H. Bailey	U.S.A., Wisconsin	*Thompson 399* (WIS)	AY779112

Table 1. Continued.

Carex species	Locality	Voucher	GenBank
Sect. *Vulpinae* (Heuffel) Christ			
C. stipata Muhl. ex Willd. var. *stipata*	U.S.A., Wisconsin	*Hipp 506* (WIS)	AY779162
Sect. *Ovales* Kunth			
Alatae group			
C. alata Torr.	U.S.A., Georgia	*Rothrock 3922* (MICH)	AY779066
C. albolutescens Schwein.	U.S.A., Ohio	*McCormac et al. 6807* (MICH)	AY779067
**C. cumulata* (L. H. Bailey) Mack.	U.S.A., Maine	*Reznicek 10924* (WIS)	AY779091
C. longii Mack.	Mexico, Umecuaro	*Zamudio et al. 11237* (MICH)	AY779115
C. ozarkana P. E. Rothrock & Reznicek	U.S.A., Arizona	*Hyatt 9357* (MICH)	AY779135
C. silicea Olney	U.S.A., Maine	*Reznicek & Reznicek 10915* (WIS)	AY779159
C. vexans F. J. Herm.	U.S.A., Florida	*Rothrock 2379* (MICH)	AY779179
Athrostachyae group			
C. athrostachya Olney	U.S.A., California	*Hipp et al. 794* (WIS)	AY779070
C. unilateralis Mack.	U.S.A., Oregon	*Wilson 5882* (MICH)	AY779177
Cyperoideae group			
**C. bohemica* Schreb.	Austria, Zwettl	*Wallnofer 13755* (WIS)	AY779073
C. sychnocephala J. Carey (1)	U.S.A., Wisconsin	*Hipp s.n.* (WIS)	AY779169
C. sychnocephala J. Carey (2)	U.S.A., Wisconsin	*Rogers 00-236* (WIS)	AY779168
Festivae group			
C. abrupta Mack.	U.S.A., California	*Hipp 799* (WIS)	AY779064
C. bonplandii Kunth	Bolivia, La Paz	*Solomon et al. 18926* (MICH)	AY779074
C. ebenea Rydb.	U.S.A., Colorado	*Hipp 1683* (WIS)	AY779095
C. gracilior Mack.	U.S.A., California	*Hipp 363* (WIS)	AY779102
C. harfordii Mack.	U.S.A., California	*Hipp 309* (WIS)	AY779104
C. haydeniana Olney	U.S.A., Utah	*Hipp 140.2* (WIS)	AY779105
**C. illota* L. H. Bailey	U.S.A., California	*Hipp & Clifton 700* (WIS)	AY779110

C. integra Mack.	U.S.A., California	*Hipp et al. 774* (WIS)	AY779111
**C. macloviana* d'Urv.	U.S.A., Wyoming	*Hipp 1893* (WIS)	AY779117
C. mariposana L. H. Bailey	U.S.A., California	*Hipp & Clifton 644* (WIS)	AY779118
**C. microptera* Mack.	U.S.A., Nevada	*Cochrane 14110* (WIS)	AY779120
C. cf. *microptera* Mack. "Pinaleno"	U.S.A., Arizona	*Hipp 2138* (WIS)	AY779086
C. cf. *microptera* Mack.	Mexico	*Reznicek 10303* (MICH)	AY779085
C. orizabae Liebm.	Mexico, Ixtapaluca	*Rzedowski 36822* (WIS)	AY779130
C. pachystachya Cham. ex Steud.	U.S.A., Utah	*Goodrich 21180* (RM)	AY779136
C. roraimensis Steyerm.	Venezuela (Roraima)	*Reznicek 11054* (MICH)	AY779152
C. stenoptila F. J. Herm.	U.S.A., Utah	*Hipp 1848* (WIS)	AY779161
C. subbracteata Mack.	U.S.A., California	*Hipp 448* (WIS)	AY779165
C. teneriformis Mack.	U.S.A., California	*Hipp & Clifton 716* (WIS)	AY779172
Festivae or Festucaceae group			
C. multicostata Mack.	U.S.A., California	*Hipp & Clifton 714* (WIS)	AY779125
C. preslii Steud.	U.S.A., Montana	*Lesica 7874* (MICH)	AY779146
C. subfusca W. Boott	U.S.A., Nevada	*Hipp 833* (WIS)	AY779167
Festucaceae group			
C. bebbii (L. H. Bailey) Fernald	U.S.A., Wisconsin	*Hipp 516* (WIS)	AY779071
**C. bicknellii* Britton var. *bicknellii*	U.S.A., Wisconsin	*Hipp 549* (WIS)	AY779072
**C. brevior* (Dewey) Mack. ex Lunell	U.S.A., Texas	*Reznicek 10345b* (MICH)	AY779075
C. cf. *brevior*	Mexico	*Reznicek 10497* (MICH)	AY779082
"Buffalo River"	U.S.A., Arkansas	*Hyatt 10461* (MICH)	AY779077
**C. crawfordii* Fernald	U.S.A., Maine	*Reznicek & Reznicek 10918* (WIS)	AY779089
C. egglestonii Mack.	U.S.A., Colorado	*Hipp 1594* (WIS)	AY779097
C. festucacea Schkuhr ex Willd.	U.S.A., Wisconsin	*Hipp et al. 561* (WIS)	AY779098
C. hyalina Boott	U.S.A., Mississippi	*Rothrock 2947* (MICH)	AY779109
**C. merritt-fernaldii* Mack.	U.S.A., New Hampshire	*Rothrock 3475* (MICH)	AY779119
**C. missouriensis* P. E. Rothrock & Reznicek	U.S.A., Missouri	*Rothrock 3567b* (MICH)	AY779121

Table 1. Continued.

Carex species	Locality	Voucher	GenBank
**C. molesta* Mack. ex Bright	U.S.A., Missouri	*Rothrock 3567.5* (MICH)	AY779122
**C. molestiformis* Reznicek & P. E. Rothrock	U.S.A., Oklahoma	*Reznicek 9766* (MICH)	AY779123
**C. normalis* Mack.	U.S.A., Wisconsin	*Rothrock & Hipp 3835* (MICH)	AY779127
C. opaca (F. J. Herm.) P. E. Rothrock & Reznicek	U.S.A., Illinois	*Reznicek 10856* (MICH)	AY779129
C. oronensis Fernald	U.S.A., Maine	*Reznicek et al. 10931* (WIS)	AY779131
C. reniformis (L. H. Bailey) Small	U.S.A., Arkansas	*Hyatt 6996* (WIS)	AY779151
C. scoparia Schkuhr ex. Willd.	U.S.A., Indiana	*Rothrock 3633b* (MICH)	AY779155
C. scoparia Schkuhr ex. Willd. var. *tessellata* Fernald & Wiegand	U.S.A., Maine	*Reznicek 10923* (WIS)	AY779156
**C. shinnersii* P. E. Rothrock and Reznicek	U.S.A., Texas	*Reznicek 10367* (MICH)	AY779157
C. straminiformis L. H. Bailey	U.S.A., Nevada	*Hipp 847* (WIS)	AY779164
**C. tenera* Dewey var. *echinodes* (Fernald) Wiegand	Canada, Ontario	*Reznicek 9509* (MICH)	AY779096
**C. tenera* Dewey var. *tenera*	U.S.A., Ohio	*Rothrock 3731* (MICH)	AY779171
C. tetrastachya Scheele	U.S.A., Texas	*Reznicek 10411* (MICH)	AY779173
C. tincta (Fernald) Fernald	U.S.A., Maine	*Rothrock 3734* (MICH)	AY779174
Fetae group			
**C. feta* L. H. Bailey	U.S.A., California	*Hipp 457* (WIS)	AY779099
C. hormathodes Fernald	U.S.A., Maine	*Reznicek 10929* (WIS)	AY779108
C. straminea Willd. ex Schkuhr	U.S.A., Wisconsin	*Hipp et al. 561* (WIS)	AY779163
C. suberecta (Olney) Britton	U.S.A., Wisconsin	*Hipp & Zimmerman 598* (WIS)	AY779166
Foeneae group			
C. adusta Boott	U.S.A., Maine	*Reznicek 10922* (WIS)	AY779065
C. arapahoensis Clokey	U.S.A., Colorado	*Hipp 1659* (WIS)	AY779068
C. argyrantha Tuck. ex Dewey	U.S.A., Maine	*Reznicek 10921* (WIS)	AY779069
C. foenea Willd.	U.S.A., Maine	*Reznicek 10928* (WIS)	AY779100
C. xerantica L. H. Bailey	Canada, Ontario	*Oldham & Bakowsky 17732* (MICH)	AY779182

Fractae group			
**C. fracta* Mack.	U.S.A., California	*Hipp 635* (WIS)	AY779101
Leporinae group			
C. leporinella Mack.	U.S.A., California	*Tallent 815* (MICH)	AY779114
C. ovalis Gooden.	New Zealand	*Ford, K.A. 30/98* (MICH)	AY779132
C. ovalis Gooden.	U.S.A., Wisconsin	*Judziewicz 6689* (WIS)	AY779133
C. ovalis Gooden.	Greece	*Strid 24872* (RSA)	AF285002
C. ovalis Gooden.	U.S.A., Oregon	*Wilson & Kuykendall 7027* (WIS)	AY779134
C. phaeocephala Piper	U.S.A., Utah	*Hipp 135* (WIS)	AY779139
C. praticola Rydb.	Canada, Ontario	*Oldham & Bakowsky 21854* (MICH)	AY779145
C. tahoensis Smiley	U.S.A., California	*Hipp 879* (WIS)	AY779170
Specificae group			
C. constanceana Stacey	U.S.A., California	*Hipp et al. 800* (WIS)	AY779088
C. davyi Mack.	U.S.A., California	*Hipp 901a* (WIS)	AY779093
C. petasata Dewey	U.S.A., Montana	*Morse & Jordan 2082* (MICH)	AY779138
**C. specifica* L. H. Bailey	U.S.A., California	*Hipp 861* (WIS)	AY779160
**C. wootonii* Mack.	U.S.A., New Mexico	*Hyatt 8294* (MICH)	AY779181
Tribuloideae group			
C. cristatella Britton	U.S.A., Wisconsin	*Hipp & Zimmerman 606* (WIS)	AY779090
**C. muskingumensis* Schwein.	U.S.A., Wisconsin	*Hipp & Biggs 2009* (WIS)	AY779126
**C. projecta* Mack.	U.S.A., Wisconsin	*Hipp et al. 1206* (WIS)	AY779147
C. tribuloides Wahlenb. var. *sangamonensis* Clokey	U.S.A., Mississippi	*Rothrock 2941* (MICH)	AY779175
C. tribuloides Wahlenb. var. *tribuloides*	U.S.A., Wisconsin	*Hipp 185* (WIS)	AY779176
Ovales—unallied			
C. cf. *lagunensis* M. E. Jones	Mexico, Durango	*Gonzalez et al. 4482* (MICH)	AY779084
C. interjecta Reznicek	Mexico, Morelos	*Zika 15398* (MICH)	AY779113
C. maackii Maxim.	Japan, Honshu	*Kan 8031* (RSA)	AY779116

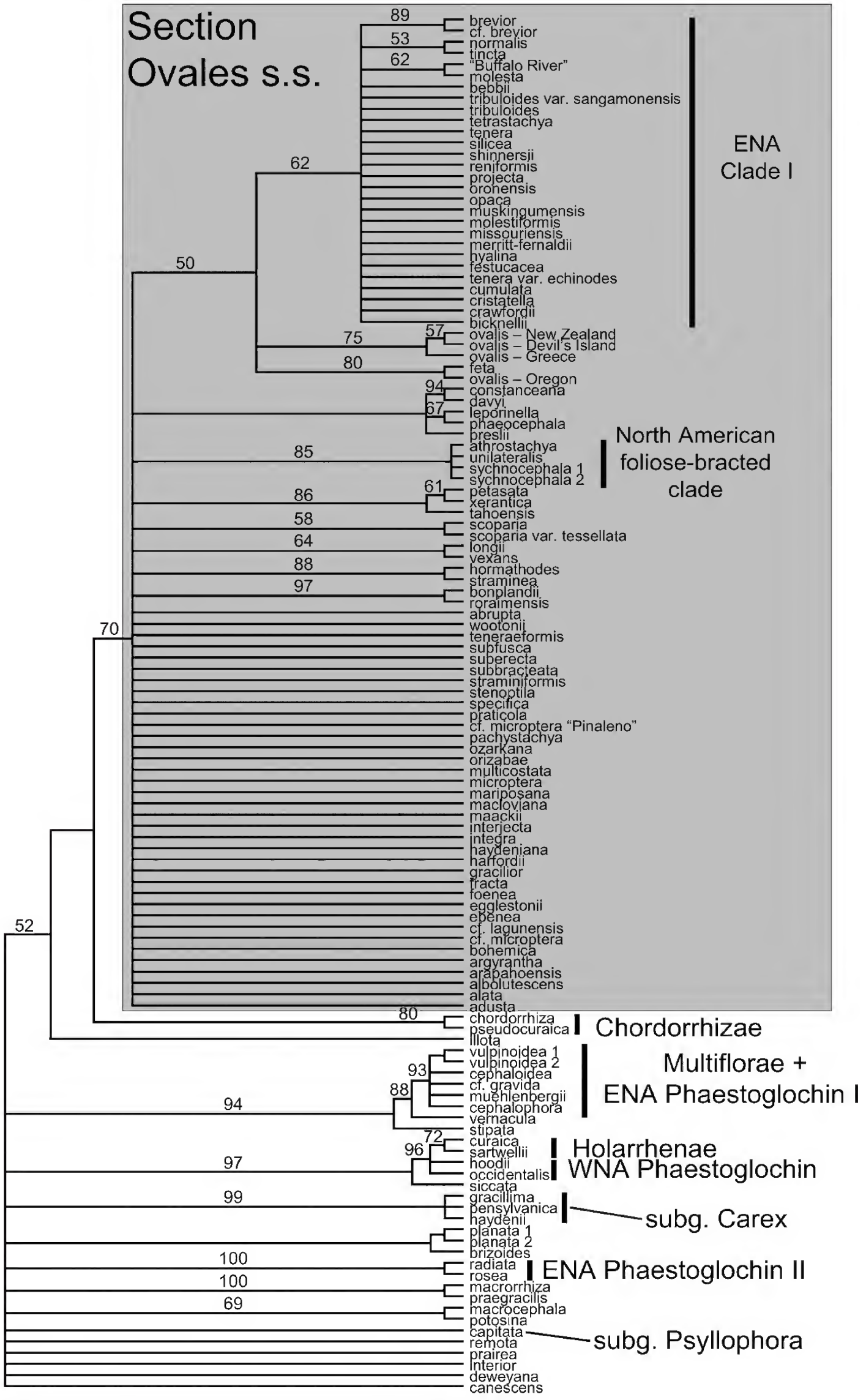

Figure 2. Strict consensus of 90,791 MP trees. Numbers above branches are nonparametric bootstrap values. Tree length (L) = 530 steps, consistency index (CI) = 0.432, retention index (RI) = 0.759.

Discussion

CIRCUMSCRIPTION OF SECTION *OVALES*

The finding that section *Ovales* is monophyletic with the exclusion of *Carex illota* reflects data from more than 90% of the species in the section. Representatives from 15 other sections of subgenus *Vignea* include all likely close relatives, including gynecandrous sections, species with winged perigynia, and species with vegetative culms. Although ITS data fail to reject the monophyly of section *Ovales* with section *Cyperoideae* excluded (WSR), phylogenetic results provide preliminary evidence for submerging *C. sychnocephala* J. Carey and *C. bohemica* Schreb. into section *Ovales*.

The East Asian *Carex maackii* has been included in section *Remotae* (Asch.) C. B. Clarke (as *Planatae* Akiyama) by at least one author (Song-Yun & Yan-Cheng, 1990), but it is generally included in section *Ovales* (Kükenthal, 1909; Reznicek, 1993; Egorova, 1999) based on its possession of winged perigynia (Fig. 1) and vegetative culms. The ITS data place *C. maackii* within section *Ovales* and weakly support its placement as sister to the rest of *Ovales*. A biogeographic hypothesis for the origin of the group is clearly premature. The position of *C. maackii* could reflect either an Old World origin for the section or a long-distance dispersal event followed by a striking lack of species diversification.

POSITION OF *OVALES* WITHIN SUBGENUS *VIGNEA*

ITS data place section *Chordorrhizae* Meinsh. sister to section *Ovales*. Another recent ITS study of subgenus *Vignea* with denser taxon sampling also recovers a clade composed of section *Chordorrhizae* and most of section *Glareosae* G. Don in a position sister to section *Ovales* (Hendrichs et al., 2004). However, these results from ITS alone are not supported by sampling using additional nrDNA and chloroplast DNA (cpDNA) regions (Hipp et al., 2006), leaving the placement of section *Ovales* in doubt. Savile and Calder's (1953) placement of *Ovales* as sister to section *Ammoglochin* is not supported. Egorova's (1999) hypothesis that section *Inversae* Kük. diverges near the base of section *Ovales* has not been evaluated.

CONVERGENCE ON VEGETATIVE CULM PRODUCTION IN SUBGENUS *VIGNEA*

Carex chordorrhiza is a circumboreal species that has traditionally been allied or considered to be conspecific with the Eurasian *C. pseudocuraica* (Hultén, 1962). Both species spread vegetatively via sprouts from the nodes of vegetative culms that behave like stolons (Hultén, 1962; Egorova, 1999). Egorova (1999) viewed this as a convergent character state and recommended splitting section *Chordorrhizae* into sections *Divisae* Christ ex Kük. (*C. chordorrhiza*) and *Holarrhenae* (*C. pseudocuraica*). The ITS data, however, support retaining *C. chordorrhiza* and *C. pseudocuraica* within a single section. This, combined with the fact that section *Holarrhenae* groups with neither section *Chordorrhizae* nor section *Ovales*, implies that there have been two or three origins of vegetative culms in subgenus *Vignea*: one within section *Holarrhenae*, and one either at the base of the clade composed of sections *Chordorrhizae* and *Ovales* (if the ITS resolution for these is correct) or at the base of each of these two sections. Late-season vegetative culms overwinter and act as stolons in three of the Tribuloideae and several of the Alatae group of section *Ovales* as well as in section *Chordorrhizae* (Eaton, 1959, 1960), and they appear to play a role in competing for light and surviving seasonal inundation in many species in which they do not act as stolons. Although the adaptive value of vegetative culms has not been evaluated using experimental methods, the independent evolution of elongate vegetative culms in several wetland sedge sections (e.g., sections *Carex*, *Chordorrhizae*, and *Holarrhenae*, as well as many species of section *Ovales*) supports the argument that vegetative culms may be adaptive in flooded habitats.

CONVERGENCE AND BIOGEOGRAPHY IN SUBGENUS *VIGNEA* AND SECTION *OVALES*

This study supports recent molecular evidence that phylogeny often correlates better with geography than with traditional taxonomy in *Carex*, both at the species level and below (Roalson & Friar, 2004; Dragon & Barrington, 2008). Monophyly of section *Phaestoglochin*, for example, is strongly rejected in this study ($P < 0.0016$), with taxa from eastern North

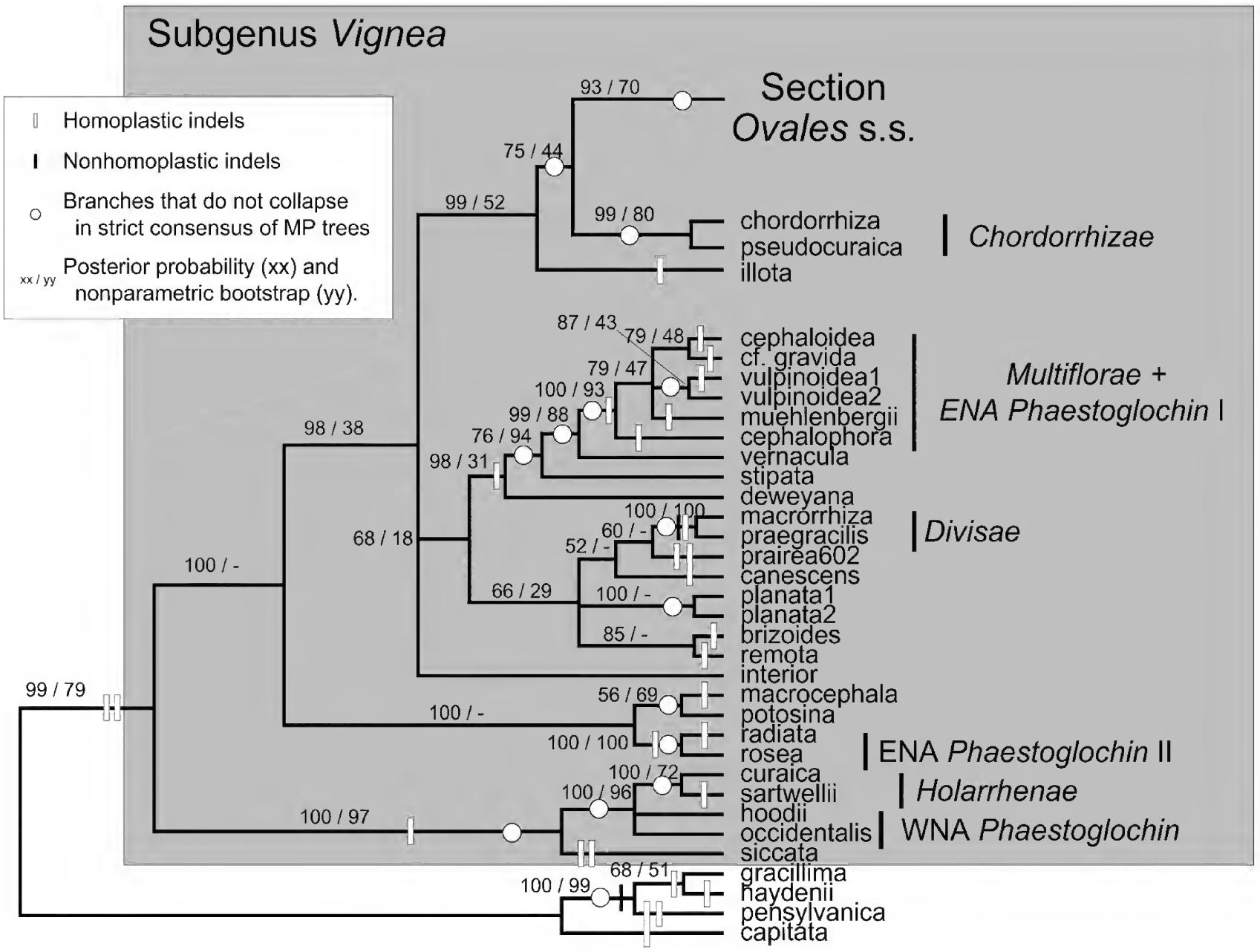

Figure 3. Bayesian majority rule consensus, part I: Subgenus *Vignea*. Numbers above branches are posterior probabilities based on sampling of 7000 trees (from 700,000 MCMC generations).

America forming two clades and western North American species forming a third. Likewise, the Old World species *C. brizoides* of section *Ammoglochin* is more closely related to two other Old World species with winged perigynia—*C. planata* and *C. remota* L.—than it is to *C. siccata*, the New World species of section *Ammoglochin*. This pattern of infrageneric taxa breaking down along geographic lines is of course not confined to *Carex* (cf. Berry et al., 2005) and will probably become more evident with increasingly detailed systematic work in the genus.

A similar pattern is seen within Mackenzie's Festucaceae group of section *Ovales*. Species in this group have flat perigynium beaks that are margined to the tip, vegetative culms with leaves clustered at the shoot apex, leaf sheaths that are hyaline on the inner face, and perigynia that are broadest at or below the middle (Rothrock & Reznicek, 2001). The Festucaceae are the most diverse of Mackenzie's species groups (21 to 24 species; Table 1), and they range from the East Coast to the West Coast (Mastrogiuseppe et al., 2002). The eastern members of the Festucaceae group form a single clade in this study, along with the Tribuloideae group and two members of the Alatae group (ENA Clade I; Figs. 2 and 4). In contrast, the species that occur strictly in the west are scattered throughout the largely unresolved western portion of the tree (Fig. 4). This suggests a single origin for the majority of the eastern species in the section and convergence in the western taxa on the complex of morphological characters that Mackenzie used to define this species group.

One of the most striking cases of convergence and biogeographic coherence in section *Ovales* pertains to the relationships of the species traditionally placed in section *Cyperoideae*. The North American member of this group, *Carex sychnocephala*, is

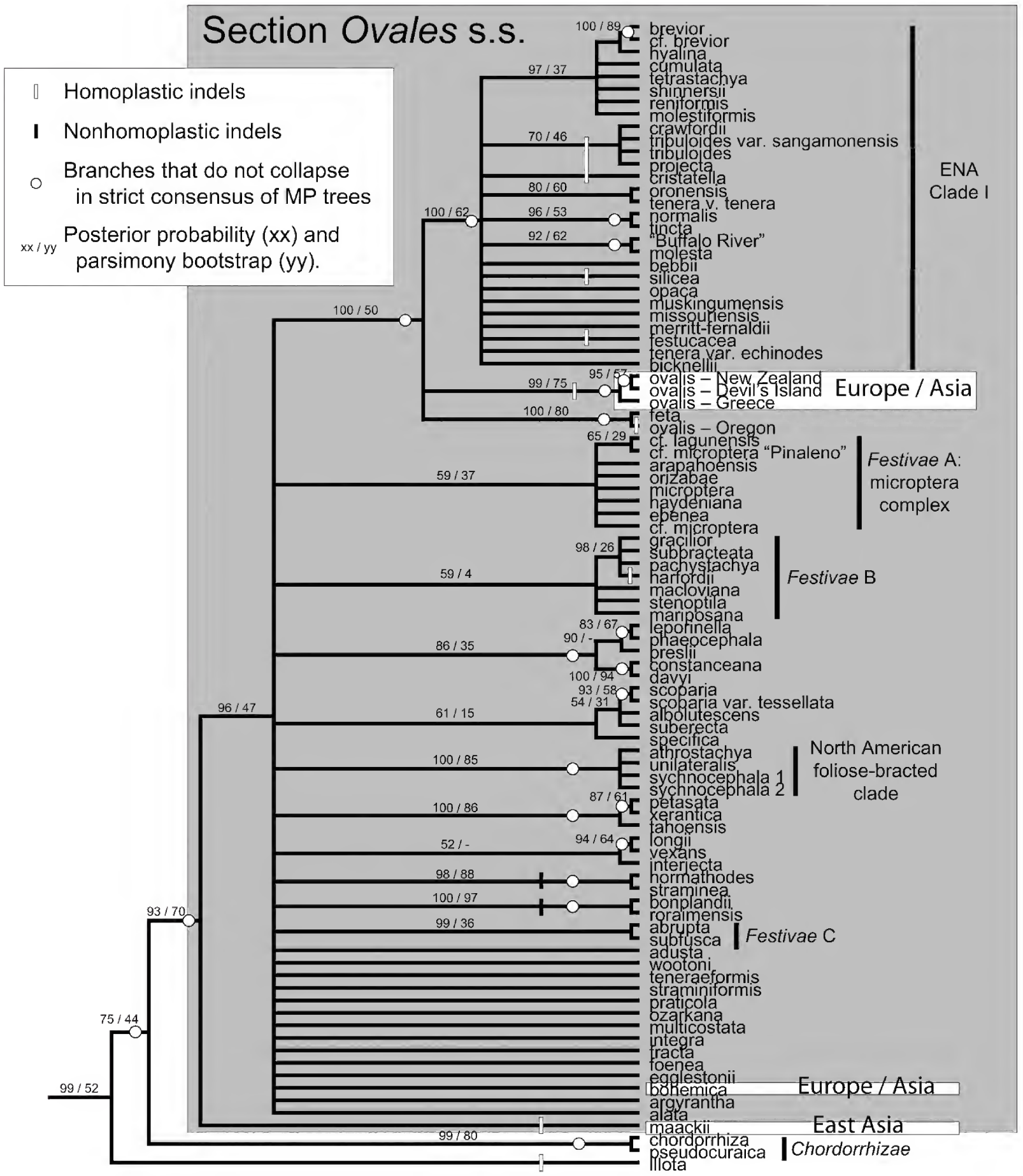

Figure 4. Bayesian majority rule consensus, part II: Section *Ovales*. Numbers above branches are posterior probabilities based on sampling of 7000 trees (from 700,000 MCMC generations).

revealed in this study to be more closely related to *C. athrostachya* Olney and *C. unilateralis* Mack. of Mackenzie's North American Athrostachyae group than to its Eurasian counterpart, *C. bohemica* (Fig. 4). This North American foliose-bracted clade of *C. sychnocephala* plus the Athrostachyae is marked by three synapomorphies: (1) prominent, foliose bracts that exceed a (2) capitate inflorescence, with (3) perigynia prominently nerved on the ventral face. However, the similarities in perigynium and bract length between *C. bohemica* and *C. sychnocephala* are far more pronounced than those that define the North American foliose-bracted clade, at least superficially (Fig. 1).

Conclusions

Section *Ovales* has long been recognized to be a natural group, but convergence in the synapomorphies that define it has not previously been investigated. This study demonstrates that the accuracy of phylogenetic hypotheses below the sectional level in *Carex* based on morphology is dependent on difficult and often subjective decisions about what characters to code and how to code them (Crins, 1990). Work under way within *Ovales* is focused on increasing phylogenetic resolution and developing comparative methods for addressing mechanisms of speciation using highly resolved phylogenies. While, 14 years after Reznicek's (1990) classic study on evolutionary trends in the genus, we are still far from "the end point, a phylogenetic classification of *Carex* to the species level" (Reznicek, 1990: 1430), fine-scale systematic work (Roalson & Friar, 2004; Hipp et al., 2007; Dragon & Barrington, 2008) is finally providing the framework needed to address biogeographic, morphological, and chromosomal patterns of speciation in this huge and ecologically important genus.

Acknowledgments

The author gratefully acknowledges Anton Reznicek and Paul Rothrock for their generosity and years of work on the taxonomy of *Carex* sect. *Ovales*. Their collections of frozen and silica-dried material permitted nearly exhaustive sampling of the eastern North American taxa in this study. My graduate advisor, Paul Berry, and my wife, Rachel Davis, were a source of advice and good humor throughout this project. I am grateful to Glen Clifton, Theodore Cochrane, Jonathan Coop, Ron Hartman, Kerry Heise, Eric Roalson, Dave Rogers, Julian Starr, Ken Sytsma, David Weixelman, Alan Yen, Elizabeth Zimmerman, and colleagues in the Sytsma and Berry labs for help in field and lab, and to the curators of MICH, MO, RM, RSA, and UC/JEPS for specimen loans. Richard Whitkus, Julian Starr, Julie Dragon, and an anonymous reviewer provided detailed and helpful comments on early drafts of this paper. This research was funded by grants from the Botanical Society of America, American Society of Plant Taxonomists, University of Wisconsin–Madison Department of Botany Davis Fund, University of Wisconsin–Madison Natural History Museums Council, a Lawrence Memorial Award from the Hunt Institute for Botanical Documentation, and National Science Foundation Dissertation Improvement Grant #0308975 to P. E. Berry and the author.

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Chapter 10

East vs. West: Monophyletic Clades Within the Paraphyletic *Carex acuta* Complex, Section *Phacocystis* (Cyperaceae)

Julie A. Dragon and David S. Barrington

ABSTRACT The *Carex acuta* L. complex, as defined by Standley, comprises 12 species from section *Phacocystis* Dumort., one of the largest sections within the genus *Carex* L. The species of the complex were originally distinguished by their nerved, stipitate perigynia with torulose bases adnate to iridescent achenes. Internal transcribed spacer (ITS) and external transcribed spacer fragment (ETS 1f) sequence data were used to test the phylogenetic integrity of the *C. acuta* complex, examine infraspecific variation within two of its polymorphic species, *C. nigra* (L.) Reichard and *C. lenticularis* Michx., and identify biogeographic patterns indicated by the phylogeny. The *C. acuta* complex was found to be paraphyletic as circumscribed. The newly discerned monophyletic groups comprise four clades: (1) an Austral–East Asian group; (2) a Eurasian clade; (3) a *C. bigelowii* Torr. ex Schwein.–*C. scopulorum* T. Holm–*C. stricta* Lam. clade; and (4) a clade of North American species, plus *C. aquatilis* Wahlenb. from Finland. Within this latter clade, western and eastern North American taxa are further divided into monophyletic groups. The two western varieties of *C. lenticularis* examined were more closely related to two Mexican taxa and the circumboreal *C. aquatilis* than they were to the eastern variety of *C. lenticularis*, which formed a clade with the amphi-Atlantic *C. rufina* Drejer. In contrast, *C. nigra* was found to be monophyletic, with little sequence divergence among American and European accessions of *C. nigra* or between them and their European allies. High infraspecific variation was found within *C. eleusinoides* Turcz. ex Kunth and *C. stricta*. Poor species circumscription and hybridization were considered as possible causes of this pattern.

KEY WORDS Biogeography, *Carex acuta* complex, ETS, ITS, phylogeny, polymorphic species, reticulate evolution, section *Phacocystis*.

The genus *Carex* L. is one of the most widespread and ecologically important of all plant genera (Reznicek, 1990). The diversity represented by this genus of approximately 2000 species has challenged systematists for over a century. Convergence and homoplasy, likely a consequence of extreme floral reduction, have hampered phylogenetic analysis and have complicated taxonomic circumscription. Given the challenges presented by morphological characters in *Carex,* systematists have increasingly turned to molecular data for increased phylogenetic resolution. The few molecular analyses completed to date have shed new light on subgeneric, sectional, and species-level relationships within *Carex* (Starr et al., 1999; Yen & Olmstead, 2000; Roalson et al., 2001). This research addresses problems of species phylogeny and delimitation in a widespread and problematic group, the *C. acuta* L. complex of section *Phacocystis* Dumort.

The *Carex acuta* complex was distinguished by Standley (1987a, b) based on the shared characters of conspicuously nerved stipitate perigynia with swollen torulose bases adnate to whitish iridescent achenes and chromosome numbers ranging from n = 42 to 46, unique within section *Phacocystis*. Roalson et al. (2001), in their analysis of sections and subgenera of *Carex* using internal transcribed spacer (ITS) and chloroplast DNA (cpDNA) sequences, included nine taxa of *Phacocystis*, three of which were members of the *C. acuta* complex. Although they found section *Phacocystis* to be paraphyletic, they provided preliminary molecular evidence that the *C. acuta* complex was monophyletic.

One of the key barriers to developing strong phylogenetic hypotheses for carices is the problem of species circumscription. In the *Carex acuta* complex, two species are prominent in this regard: *C. lenticularis* Michx. and *C. nigra* (L.) Reichard. Both taxa are highly variable morphologically depending on their habitat, elevation, and latitude. Where morphs overlap, intermediate populations are often found. While no confirmed hybrids involving *C. lenticularis* have been identified, *C. nigra* has been shown to produce fertile hybrids with a number of species of section *Phacocystis*, including *C. acuta*, *C. elata* All., *C. bigelowii* Torr. ex Schwein., *C. stricta* Lam., and *C. aquatilis* Wahlenb. (Faulkner, 1972, 1973). Thus both phenotypic variation and hybridization are possible explanations for the taxonomic complexity of these species.

The goal of the research described here was to use cladistic analysis of the ITS region and an external transcribed spacer fragment (ETS 1f) of ribosomal DNA (rDNA) to elucidate the phylogeny of the species placed in the *Carex acuta* complex. Our specific objectives were to (1) test the monophyly of the complex, (2) assess the infraspecific variation within the highly polymorphic species *C. nigra* and *C. lenticularis*, and (3) interpret biogeographic history in the light of the retrieved phylogeny.

Materials and Methods

SAMPLING

Forty-one accessions representing 23 species were included in the analysis. Voucher data and GenBank accession numbers for all accessions are provided in Table 1. All the members of Standley's *Carex acuta* complex were sampled, with the exception of *C. decidua* Boott from South America and *C. cuchumatanensis* Standl. & Steyerm. from Guatemala, for a total of 10 species.

Because the choice of outgroup taxa was problematic, we chose a diversity of taxa that might be expected to be sister groups to the *Carex acuta* complex. The outgroup taxa we sampled fall into three groups. First, we sampled five taxa from section *Phacocystis*. Two additional unnamed Mexican taxa that share morphological features with the members of section *Phacocystis* and the *C. acuta* complex were also included in this first group. Second, following the suggestion of Standley (1987a) that the taxa of section *Bicolores* Tuck. were sister to those of the *C. acuta* complex, *C. bicolor* All. and *C. aurea* Nutt. were included as outgroup taxa. Third, taxa of other sections that share morphological features with members of section *Phacocystis* were also sampled. These include (1) *C. lemanniana* Boott and *C. donnell-smithii* L. H. Bailey (Central America) of section *Fecundae* Kük., and (2) the North American *C. bella* L. H. Bailey of section *Racemosae* G. Don and the amphi-Pacific *C. podocarpa* R. Br. of section *Scitae* Kük. *Carex podocarpa* was especially important to include in this study because Roalson et al. (2001) found it to be inserted within section *Phacocystis*.

DNA EXTRACTION AND SEQUENCING

Total genomic DNA was extracted from fresh material using the DNEasy Plant Mini Kit (Qiagen, Valencia, California), and from silica-dried material with a CTAB buffer following the protocol of Doyle and Doyle (1987).

The polymerase chain reaction (PCR) was used to amplify ITS and 5.8S rDNA using a 1:1 ratio of primers ITS-4 (White et al., 1990) and AB101 (Sun et al., 1994) (Table 3). Each 25-µl reaction mixture contained 2.5 µl of 10× reaction buffer, 5 µl of 5× Q-solution (Qiagen, Valencia, California), 0.5 µl dNTPs (10 mM each), 1.25 µl of both primers (10 µM concentrations), 0.125 µl *Taq* (5 units/µl), 23.75 µl ddH_2O, and 10–50 ng of DNA template. Double-stranded PCR products were produced in an Amplitron II Thermolyne thermocycler (Barnstead, Dubuque, Iowa). The DNA was pretreated at 96°C for two minutes followed by 32 cycles of DNA denaturation at 96°C for one minute, primer annealing at 50°C for one minute, and DNA strand extension by *Taq* DNA polymerase at 72°C for two minutes. The PCR was terminated by a final extension of 72°C for seven minutes.

PCR was also used to amplify the 3′ end of the ETS-1f using a 1:1 ratio of primers ETS-1F and 18S-R (Starr et al., 2003; see Table 3). Each 25-µl reaction mixture contained 1.25 µl of 100% glycerol, 11.5 µl of 100 mM KCl, 2.3 µl of 100 mM Tris HCl, 2.3 µl of 25 mM $MgCl_2$, 3.8 µl of 5× Q-solution (Qiagen, Valencia, California), 0.575 µl dNTPs (10 mM each), 0.575 µl of both primers (20 µM concentrations), 0.125 µl *Taq* (5 units/µl), and 10–50 ng of DNA template. Double-stranded PCR products were produced on an Amplitron II Thermolyne thermocycler (Barnstead, Dubuque, Iowa). The DNA was pretreated at 97°C for one minute followed by 40 cycles of DNA denaturation at 97°C for 10 seconds, primer annealing at 55°C for 30 seconds, and DNA strand extension by *Taq* DNA polymerase at 72°C for 20 seconds plus four additional seconds per cycle. The PCR was terminated by a final extension of 72°C for eight minutes.

The PCR products were electrophoresed on 1% agarose gels in 1× TBE buffer (pH 8.0). The gels were then stained with ethidium bromide and the DNA excised from the gels. A Qiaquick PCR Purification Kit (Qiagen, Valencia, California) was used to elute the DNA from the gels. Dye-terminator reaction mixtures of 20 µl were made with the purified DNA templates. The reactions were pretreated in the thermocycler for five minutes at 96°C. Cycle sequencing of the reactions comprised 25 cycles of DNA denaturation at 96°C for 10 seconds, primer annealing at 50°C for five seconds, and DNA strand extension by *Taq* DNA polymerase at 60°C for four minutes. Cycle sequencing of ITS 1 used the external sequencing primers ITS-L and internal sequencing primer ITS-2, while cycle sequencing of ITS 2 used external sequencing primer ITS-4 and ITS-3 (Table 3) (White et al., 1990; Hsiao et al., 1994). Cycle sequencing of ETS 1f used the same primers used in PCR. Automated sequencing was used to process the amplified templates (Vermont Cancer Center, Burlington, Vermont). Sequence chromatograms were proofed by inspection and edited using Sequence Navigator 1.0 (Perkin-Elmer, Wellesley, Massachusetts). Sequences were initially aligned by Sequence Navigator, followed by additional alignment by inspection. The aligned sequence data were analyzed for biases and ambiguities. Indels were coded as present or absent and incorporated into the sequence data. The poly-A tail at the 3′ end of ITS 1 was excluded from pairwise sequence-divergence and phylogenetic analysis. A single potentially informative site from the 5′ end of 5.8S was included in the analyses. Ambiguous nucleotides were scored as such in the data set.

PHYLOGENETIC ANALYSIS

Maximum parsimony was used to conduct a heuristic search for the shortest trees using PAUP 4.0beta8a (Swofford, 1998). We conducted this search by simple addition of 29 taxa for 500 replicates to search for islands of equally most parsimonious trees. Using tree bisection-reconnection (TBR) branch swapping, the resulting trees were swapped to completion, holding 10 trees at each stepwise addition to a maximum of 100,000 trees. Bootstrap values (BS) were determined for 1500 replicates (heuristic searches, TBR branch swapping, simple taxon addition) to assess the support for the clades identified. A separate analysis of each marker was conducted to test the level of incongruence between them. Incongruence was assessed using a partition homogeneity test and by directly comparing the

Table 1. Accession vouchers with taxon, locality, voucher information, and GenBank accession number.

Taxon	Origin	Voucher information	GenBank accession no. ITS/ETS
Carex acuta complex sensu Standley (1987a, Standley et al., 2003), section _Phacocystis_			
C. acuta L.	U.S.S.R., Siberia	*Elias et al. 8254* (RSA)	AF284892, AY770434
C. elata All.	SWEDEN, Uppland	*L. Thorán 1363* (S)	AY770470, AY770440
C. eleusinoides Turcz. ex Kunth (SIB1)	U.S.S.R., Buryatskaya	*Elias 12025* (RSA)	AF285006, AY770441
C. eleusinoides Turcz. ex Kunth (MONG1)	MONGOLIA	*S. Young s.n.* (VT)	AY770471, AY770442
C. hermannii Cochrane	MEXICO, Volcán Ixtaccíhuatl	*M. Sundue 388* (VT)	AY770473, AY770444
C. gaudichaudiana Kunth	NEW ZEALAND, Waiuta	*K. A. Ford 28/98* (VT)	AY770472, AY770443
C. lenticularis Michx. var. *lenticularis* (VT1)	U.S.A., Vermont	*J. Dragon 00-1c* (VT)	AY770475, AY770447
C. lenticularis Michx. var. *lenticularis* (MI1)	U.S.A., Michigan	*D. Henson 1788* (WIS)	
C. lenticularis Michx. (MI2)	U.S.A., Michigan	*A. Arez et al. 8265* (WIS)	
C. lenticularis Michx. var. *lipocarpa* (T. Holm) L. A. Standl. (OR1)	U.S.A., Oregon	*M. Thompson 95154* (VT)	AY770476, AY770448
C. lenticularis Michx. var. *lipocarpa* (T. Holm) L. A. Standl. (WA1)	U.S.A., Washington	*D. Barrington 2091* (VT)	AY770477, AY770449
C. lenticularis Michx. var. *impressa* (L. H. Bailey) L. A. Standl.	U.S.A., California	*B. Ertter 10424* (WSP)	AY770474, AY770445
C. nigra (L.) Reichard (MI1)	U.S.A., Michigan	*A. Reznicek s.n.* (VT)	
C. nigra (L.) Reichard (ME1)	U.S.A., Maine	*A. Dibble 9800* (VT)	AY770480, AY770452
C. nigra (L.) Reichard (IC1)	ICELAND, Akureyri	*H. Kristinnsson s.n.*	AY770481, AY770453
C. nigra (L.) Reichard (SU1)	SWEDEN, Södermanland	*F. Lind s.n.* (S)	AY770482, AY770454
C. nigra (L.) Reichard (SU2)	SWEDEN, Uppland	*L. Thorán 2426* (S)	AY770483, AY770455
C. nigra (L.) Reichard subsp. *juncella* (Fries) Á. Löve & D. Löve	SWEDEN, Lappland	*A. Anderberg 2092* (S)	AY770484, AY770456
C. rufina Drejer (IC1)	ICELAND, Leirdalsheiði	*H. Kristinnsson s.n.*	AY770485, AY770458

C. rufina Drejer (SU1)		SWEDEN, Lappland	*A. Anderberg 2548* (S)	
C. thunbergii Steud. (KI2)		RUSSIA, Kharimhotan	*B. Semsrott 0193* (WTU)	AY770488, AY770462
C. thunbergii Steud. (KI3)		RUSSIA, Makamushi	*B. Semsrott 1561* (WTU)	AY770489, AY770463
C. thunbergii Steud. (KI6)		RUSSIA, Paramushi	*S. Gage 4333* (WTU)	
C. trinervis Degl.		BELGIUM, De Panne	*R. Viane s.n.* (VT)	AY770491, AY770465
Outgroup taxa, section *Phacocystis* Dumort.				
C. aquatilis Wahlenb. (FI1)		FINLAND	*Kukonen 12828* (RSA)	AF284892, AY770435
C. aquatilis Wahlenb. var. *substricta* Kük. (VT1)		U.S.A., Vermont	*J. Dragon 02-70* (VT)	AY770467, AY770436
C. bigelowii Torr. ex Schwein.		U.S.A., Vermont	*J. Dragon 02-1b* (VT)	AY770469, AY770438
C. scopulorum T. Holm var. *scopulorum*		U.S.A., Nevada	*Holmgren & Reveal 1601* (RSA)	AF285056, AY770459
C. sp. (MX1)		MEXICO, Pueblo Nuevo	*A. A. Reznicek & S. González 11147* (VT)	AY770478, AY770450
C. sp. (MX2)		MEXICO, Pueblo Nuevo	*A. A. Reznicek & S. González 11141* (VT)	AY770479, AY770451
C. stricta Lam. (VT1)		U.S.A., Vermont	*J. Dragon 02-73* (VT)	AY770486, AY770460
C. stricta Lam. (NH1)		U.S.A., New Hampshire	*Barrington s.n.* (VT)	AY770487, AY770461
C. torta Boott		U.S.A., Vermont	*J. Dragon 1a* (VT)	AY770490, AY770464
Outgroup taxa, other sections				
C. bella L. H. Bailey	section *Racemosae*	U.S.A., New Mexico	*Roalson 823* (NMCR)	AF284966 (ITS only)
C. podocarpa R. Br.	section *Scitae*	U.S.S.R., Magadan Oblast	*Elias 11380* (RSA)	AF284998, AY770457
C. aurea Nutt.	section *Bicolores*	U.S.A., California	*DeDecker 5606* (RSA)	AF285062 (ITS only)
C. bicolor All. (JBQ1)	section *Bicolores*	CANADA, Québec, James Bay	*J. Dragon 00-56* (VT)	AY770468, AY770437
C. bicolor All. (IC1)	section *Bicolores*	ICELAND, Hólsfjöll	*Kristinnsson 21663* (AMNH)	
C. bicolor All. (SU1)	section *Bicolores*	SWEDEN, Lappland	*B. & K. Bremer 2169* (S)	
C. donnell-smithii L. H. Bailey	section *Fecundae*	MEXICO, Chiapas	*Shilom Ton 8199* (RSA)	AF285005, AY770439
C. lemanniana Boott	section *Fecundae*	COSTA RICA, Páramo de las Vuettas	*M. Sundue et al. 389* (VT)	AY770446 (ITS only)

topological differences between the ITS and ETS 1f trees.

In addition to maximum parsimony, maximum likelihood was also employed. The HKY + I + G model of evolution was found by Modeltest 3.06 (Posada & Crandall, 1998) to best explain the data. This model accounts for the unequal distribution of transitions to transversions [transition/transversion ratio = 3.1156 (kappa = 6.3930346)] and base frequencies (A = 0.17210, C = 0.29780, G = 0.29170, T = 0.23840), and a continuous (gamma) distribution of among-site rate variation (proportion of invariable sites = 0.5513, shape parameter alpha = 0.7323) within the data. This model was used to generate corrected distances and a maximum likelihood tree. Bootstrap analysis (heuristic searches, TBR, simple taxon addition) of 200 replicates was used to determine the statistical support for the branches of the maximum likelihood tree.

Results

Sequence Analysis

The ranges and average lengths of ITS 1, ITS 2, and ETS 1f from the data set were similar to those found in other carices (Starr et al., 1999, 2003, 2008; Table 2). Twenty-six of 446 positions in the ITS sequence data had double nucleotides at a single site. These were inferred to be heterozygous nucleotides. Seven of these heterozygous nucleotides occurred at phylogenetically informative positions. In the ETS 1f sequences, 28 of 560 positions were inferred to be heterozygous. Of those, six occurred at phylogenetically informative positions. Of the 13 phylogenetically informative heterozygous nucleotides in the combined data set, four belonged to *Carex stricta* (VT1) (one from ETS 1f and three from ITS) and four to *C. bigelowii* (two from each marker). The remainder were distributed singly among five other taxa (three from ETS 1f and two from ITS).

Phylogenetic Analysis

Alignment of the sequence data yielded 1023 characters, 447 characters from ITS, and 567 from ETS 1f. ITS yielded 70 variable characters, 38 of which were phylogenetically informative (29 transitions; eight transversions; one indel), and 32 of which were autapomorphies. ETS 1f sequence data yielded 561 characters, of which 80 were variable, with 37 phylogenetically informative (26 transitions and 10 transversions; one indel), and 43 autapomorphies. See Table 2 for a summary of the ITS and ETS 1f sequence data.

Initial analysis of ITS sequence data indicated that among the outgroup taxa, the members of section *Bicolores* and *Carex bella* of section *Racemosae* were the most divergent. They therefore were omitted from further data collection and analysis. Among the remaining outgroup taxa, the two accessions of section *Fecundae* (*C. donnell-smithii* and *C. lemanniana*) and one of the unnamed Mexican taxa (which we called MX2) were the most divergent from the ingroup taxa; we used these three taxa to root all subsequent trees.

Two most parsimonious trees, of 215 steps (consistency index [CI] = 0.730, retention index [RI] = 0.808, homoplasy index [HI] = 0.270), were identified. The strict consensus of the two trees reveals the *Carex acuta* complex to be paraphyletic, with its members divided into two major clades, both of which include additional taxa from section *Phacocystis*, including *C. aquatilis*, *C. stricta*, *C. bigelowii*, and *C. scopulorum* T. Holm (Fig. 1). Sister to these two clades is *C. podocarpa* currently of section *Scitae*. The analysis did, however, identify the following four clades that can be characterized on the basis of the geographic distribution of their taxa: (1) a Eurasian clade, consisting of the Eurasian taxa of the *C. acuta* complex, including the amphi-Atlantic *C. nigra* (100% BS); (2) a *C. bigelowii–stricta* clade, comprising the circumpolar *C. bigelowii*, its close Pacific North American relative *C. scopulorum*, and the eastern North American *C. stricta* (99% BS); (3) a North American clade, including the American taxa of the complex plus the circumpolar *C. aquatilis* (65% BS); and (4) an Austral–East Asian clade, a clade of three taxa from the complex, two of which are from East Asia and one from New Zealand (< 50% BS). Within the North American clade, several smaller clades were resolved, including (1) the lenticularis–rufina clade, a clade of *C. lenticularis* var. *lenticularis* and *C. rufina* Drejer (100% BS); (2) the lipocarpa–impressa clade, including *C. lenticularis* var. *lipocarpa* (T. Holm) L. A. Standl., *C. lenticularis* var. *impressa* (L. H. Bailey) L. A. Standl., and MX1 (64% BS); and (3) a *C. aquatilis* clade, comprising *C. aquatilis* and *C. aquatilis* var. *substricta* Kük. (95% BS). Variation

Table 2. Summary statistics for ITS 1, ITS 2, and ETS 1f spacer regions. TI = transitions; TV = transversions.

	ITS 1	ITS 2	ETS 1f
Aligned length (bp)	219	227	560
Length range (bp)	216–219	223–227	553–560
Length average (bp)	217.4	225.9	557.9
GC content range	135–143	151–161	307–324
GC content average	138.78 (63%)	156.13 (69%)	317.36 (57%)
No. of variable sites	30	40	80
No. of phylogenetically informative sites	13 (10 TI; 2 TV; 1 indel)	15 (19 TI; 6 TV)	37 (26 TI; 10 TV; 1 indel)
No. of autapomorphies	17	25	43

between the two most parsimonious trees is due entirely to the unresolved relationship between three of the accessions of *C. nigra*. The maximum likelihood tree shows slightly stronger support for the sister relationship of the Eurasian and *C. bigelowii* clades (54%) found in the maximum-parsimony consensus tree, but slightly weaker support for the North American clade (68%). There were no topological differences between the maximum parsimony consensus tree and the maximum likelihood tree.

The data provided by the two DNA markers were found to be significantly incongruent. Analyzing ETS 1f alone, the same tree topology as that of the combined data set was found. ITS alone alternates the placement of the Austral–East Asian and *Carex bigelowii–stricta* clades, and places *C. gaudichaudiana* Kunth basal to the North American clade and *C. stricta* in a more derived position sister to *C. aquatilis* (data not shown).

INFRASPECIFIC VARIATION

Total pairwise sequence divergence in the taxa examined ranged from 0.10% to 5.58% under the HKY + I + G model for estimating the number of nucleotide substitutions. Low infraspecific sequence divergence was found among six accessions of *Carex nigra* (0.10% to 0.51%), although even less divergence was found between some accessions of *C. nigra* and three European taxa (0.10% to 0.30%). While overall divergence was higher among the four accessions of *C. lenticularis* (0.20% to 1.71%), greater sequence divergence was found among some accessions of *C. lenticularis* than between them and their nearest allies (0.20% to 1.94%), just as in *C. nigra*.

Multiple accessions of a few taxa had identical ITS and ETS 1f sequences, including three accessions of *Carex lenticularis* var. *lenticularis*, two North American accessions of *C. nigra* (ITS only), two accessions of *C. rufina*, and two accessions of *C. thunbergii* Steud. from the Kuril Islands (KI3 and KI6). Other taxa for which multiple accessions were sequenced did not have identical ITS and ETS 1f sequences, including accessions of *C. eleusinoides* Turcz. ex Kunth with 1.15% sequence divergence, *C. lenticularis* var. *lipocarpa* with 0.20% sequence divergence, *C. thunbergii* with 0.20% sequence divergence, and *C. stricta* with 1.39% sequence divergence. It is important to note that different accessions of *C. eleusinoides* and *C. stricta* created topologically different trees (data not presented). While only one accession of each of these species was included in this study, the implications of including these divergent individuals in phylogenetic analyses are discussed in more detail below.

DISCUSSION

MONOPHYLETIC GROUPS AND SISTER RELATIONSHIPS WITHIN SECTION *PHACOCYSTIS*

Our first objective was to test the phylogenetic integrity of the *Carex acuta* complex. The evidence provided by ITS and ETS 1f sequence data shows that the *C. acuta* complex, as circumscribed by Standley (1987a, b) is paraphyletic. The larger clade

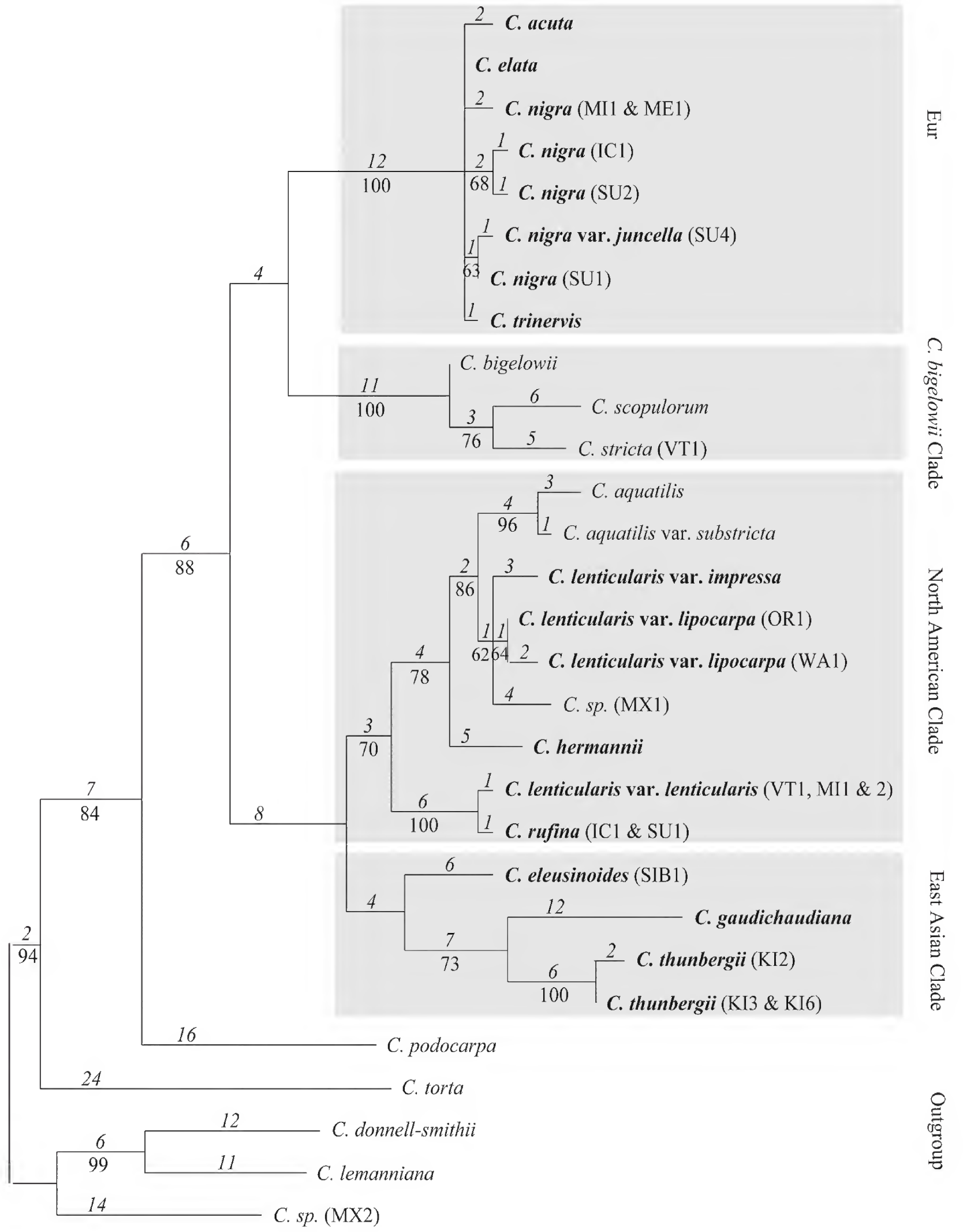

Figure 1. One of the two most parsimonious trees (length = 214; CI = 0.73; RI = 0.81; HI = 0.27). Numerals above the branches are branch lengths. Numerals below the branches are > 50% bootstrap estimates. Clade names are written vertically to the right of the corresponding clades. Taxa of the *Carex acuta* complex are in bold.

Table 3. Primer sequences used to amplify the rDNA internal transcribed spacers (ITS 1 and ITS 2) and a portion of the ETS between the tandem repeats of the 18S and 26S genes (ETS 1f).

Primer reference	Primer sequence
Forward primer ITS-L (Hsiao et al., 1994)	5′-TCGTAACAAGGTTTCCGTAGGTG-3′
Forward primer AB101 (Sun et al., 1994)	5′-ACGAATTCATGGTCCGGTGAAGTGTTCG-3′
Reverse primer ITS-4 (White et al., 1990)	5′-TCCTCCGCTTATTGATATGC-3′
Internal forward primer ITS-3 (White et al., 1990)	5′-GCATCGATGAAGAACGCAGC-3′
Internal reverse primer ITS-2 (White et al., 1990)	5′-GCTGCGTTCTTCATCGATGC-3′
Forward primer ETS-1F (Starr et al., 2003)	5′-CTGTGGCGTCGCATGAGTTG-3′
Reverse primer 18S-R (Starr et al., 2003)	5′-AGACAAGCATATGACTACTGGCAGG-3′

that includes all of the taxa of the *C. acuta* complex also includes four taxa from elsewhere in section *Phacocystis* (*C. aquatilis*, *C. bigelowii*, *C. scopulorum* var. *scopulorum*, and *C. stricta*; Fig. 1). Sister to this clade is *C. podocarpa* of section *Scitae*. The placement of *C. podocarpa* basal to this clade separates *C. torta* Boott from the rest of the members of section *Phacocystis*. While our data set includes only 20% of the species of section *Phacocystis*, our results suggest that either *C. torta* has been wrongly placed in section *Phacocystis* or that *Phacocystis* should include *C. podocarpa*. Species traditionally placed in the *C. acuta* complex are divided among four monophyletic groups. Three of these putative clades can be distinguished by their geographic distribution: Eurasian, Austral–East Asian, and North American (minus *C. bigelowii*, *C. scopulorum*, and *C. stricta*). The North American clade can be further subdivided into two clades, one with taxa of western distribution, and the other with taxa of eastern affinities. The geographic integrity of the majority of the clades identified thus far provides support for the phylogenetic history inferred from our study.

INFRASPECIFIC VARIATION

Our second objective was to examine infraspecific variation within two of the polymorphic taxa of the ingroup, *Carex lenticularis* and *C. nigra*. In the case of *C. lenticularis* and *C. nigra* and their allies, a recasting of species lineages may be in order. In addition, high infraspecific divergence was found among accessions of *C. eleusinoides* and *C. stricta*. In their case, the variation suggests a more complicated phylogenetic history.

Carex lenticularis

The molecular divergence between three of the varieties of the North American *Carex lenticularis* is consistent with their taxonomic recognition. However, the eastern variety *lenticularis* forms a well-supported clade with the amphi-Atlantic *C. rufina*, while the two western taxa, varieties *lipocarpa* and *impressa*, form a well-supported clade with one of the unnamed Mexican accessions (MX1). These results suggest that the western and eastern varieties of *C. lenticularis* either pertain to different species or are part of a much more broadly circumscribed *C. lenticularis*. The biogeographic pattern implied by the phylogeny suggests that there are isolated lineages in the western cordillera and Mexico and in eastern North America, a pattern also detected by Hipp (2008) in *Carex* sect. *Ovales* Kunth.

Carex nigra

In North America, populations of *Carex nigra* display some morphological variation, but are nonetheless interpreted as one species (Standley, 1987a). In the present study, the two North American accessions of *C. nigra* (from Maine and from a disjunct population in Michigan) share identical ITS and ETS 1f sequences, supporting the integrity of the species in North America. In contrast, we found varying amounts of sequence divergence when we considered the North American material in comparison with the Icelandic and European accessions (0.2% to 0.4%). Across Europe and Asia, the group of *C. nigra* is highly variable, leading to the recognition of closely allied segregate species and subspecies. Despite their morphological variation and

taxonomic status as species, the European taxa *C. acuta*, *C. trinervis* Degl., *C. nigra*, and *C. elata* exhibit little sequence divergence from one another (0.1% to 0.3%), and less variation than is found within *C. nigra*. The clade including *C. nigra* and its allies is genetically and morphologically more diverse in Europe than in eastern North America. It may be that the assemblage is a single variable species whose biogeographic history is fundamentally European, and that the North American populations are recent arrivals by long-distance dispersal or human introduction.

Carex eleusinoides

The two accessions of *Carex eleusinoides*, both from the tundra in the mountains near Lake Baikal, diverge by 1.15%. Although the two are phenetically most similar to one another in our analysis, separate phylogenetic analyses including the two accessions yield different results. The Siberian accession (SIB1) is sister to a clade that includes *C. gaudichaudiana* and *C. thunbergii* (Fig. 1), while the Mongolian accession (MONG1) is sister to *C. lenticularis* (data not shown). A phylogenetic analysis that included both accessions yielded a tree with decreased resolution and lower CI and RI values (data not shown). These observations suggest that *C. eleusinoides*, as currently circumscribed, may be polyphyletic.

Carex stricta

The sequences from the two accessions of *Carex stricta* differ by 1.39%, one of the largest distances so far encountered for accessions of a single species of *Carex*. When analyzed separately within the data set, the accession from ca. 200 m in Vermont is sister to *C. scopulorum* var. *scopulorum* (Fig. 1) from Nevada, while the accession from ca. 800 m in New Hampshire forms a weakly supported clade with eastern North American *C. aquatilis* var. *substricta* (data not shown). When both are included in the parsimony analysis they form a weak clade with each other, sister to the *C. bigelowii–scopulorum* clade, but support for all nodes in the North American clade is greatly reduced (data not shown).

RETICULATE EVOLUTION AND INFRASPECIFIC VARIATION

Considering the data on infraspecific variation our samples fall into two sets. On the one hand, *Carex nigra* and *C. lenticularis* appear to harbor substantial variation but, with adjustment of taxonomic species limits, may be possible to circumscribe as natural species. In contrast, *C. eleusinoides* and *C. stricta* each comprise a pair of accessions that lie distant in separate phylogenetic analyses and decrease measures of tree resolution and support in combined analyses (data not shown). These accessions are also among the richest in ambiguous (two-nucleotide) sites in the data. Thus, hybridization, the presence of paralogous sequences, and variation between copies of ITS and ETS 1f need to be explored as possible explanations of our results. *Carex stricta* is reported to hybridize with *C. aquatilis* and *C. nigra* based on observations of anomalous morphology within some sympatric populations (Standley, 1989; Standley et al., 2003). Similar evidence suggests that the formation of hybrids is frequent in section *Phacocystis*, particularly in salt marshes and along brackish waterways (Cayouette & Morisset, 1985; Standley et al., 2003). In our work, as in most molecular phylogenetic work, the habit of collecting accessions in mature fruit for morphological determination precludes the assembly of meiotic and pollen material critical in hybrid analysis. A more intensive approach, involving either (1) the cultivation of plants to allow for both cytological and molecular work, or (2) sequencing of clonal DNA derived from candidate-hybrid accessions, would yield the evidence necessary to discern hybrids in the data set. At the same time, the latter approach would distinguish ambiguous nucleotides in different genomes (as a result of hybridization) from those in different copies of ITS or ETS in the same genome (from a failure of concerted evolution in these sequences).

FUTURE RESEARCH

Future research into the systematics of section *Phacocystis* will include additional sampling within the section in order to test the monophyly of the clades identified in this study, and to increase understanding of the relationship among taxa within the section as a whole. Particular emphasis will be placed on the North American clade, which includes *Carex lenticularis* and its allies, and *C. aquatilis*, and will include an examination of the morphological characters that are common to both taxa, and further examination of the biogeographic patterns presented by the data.

The role of reticulation in the diversification of section *Phacocystis* requires additional attention.

For this study ITS and ETS markers will require cloning, and a comparison of nuclear to chloroplast markers would be useful. Additional crossing experiments and chromosome analyses, such as those conducted by Faulkner (1972, 1973) and Cayouette and Morisset (1985) could also provide further witness to the relationships among taxa and the role hybridization has played in the diversification of this morphologically complex group.

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Chapter 11

Carex Sect. *Phyllostachyae*: The Value of a Multidisciplinary Approach in Conducting Systematics Studies in Sedges

Bruce A. Ford, Robert F. C. Naczi, and Julian R. Starr

ABSTRACT Over the past 20 years, taxonomic novelties within *Carex* L. have been discovered at an unprecedented rate. For the most part, discovery has been a gradual process involving the analysis of existing specimens and the use of a variety of data sources. Our studies of *Carex* sect. *Phyllostachyae* Tuck. ex Kük. serve as a striking example of this recent pattern of discovery. A detailed examination of herbarium specimens and extensive fieldwork alerted us to the presence of significant taxonomic variation. Macro- and micromorphologic, anatomic, genetic, and phytogeographic data were then used to test our initial taxonomic hypotheses. As a result of our research, the number of species now recognized in section *Phyllostachyae* doubled over a 10-year period. Our clarified understanding of species limits allowed the generation of phylogenetic hypotheses that were unencumbered by a poorly resolved taxonomy. Cladistic analyses of sequences from the internal and external transcribed spacer regions of nuclear ribosomal DNA, plus morphologic data, have shown that section *Phyllostachyae* is monophyletic and is composed of three clades. Scales that do not conceal the perigynia, filiform stigmas, and relatively large numbers of staminate flowers characterize the narrow-scaled clade (*C. basiantha* Steud., *C. jamesii* Schwein., *C. juniperorum* Catling, Reznicek & Crins, *C. superata* Naczi, Reznicek & B. A. Ford, *C. timida* Naczi & B. A. Ford, *C. willdenowii* Willd.), while species in the wide-scaled clade (*C. backii* Boott in Hook., *C. cordillerana* Saarela & B. A. Ford, *C. saximontana* Mack.) are distinguished by pistillate scales that conceal the perigynia, thick stigmas, and relatively small numbers of staminate flowers. *Carex latebracteata* Waterf., with its much larger perigynia, absence of lateral spikes, and tightly coiled stigmas, is sister to both the wide- and narrow-scaled clades. Our studies emphasize the benefits of a sectional-level investigation and the advantage of a multidisciplinary approach to systematics studies in sedges. Our research also provides suggestions for future systematics research on *Carex*.

KEY WORDS *Carex* sect. *Phyllostachyae*, multidisciplinary research, new species, phylogeny, systematics.

The genus *Carex* L. offers exceptional challenges for systematics research. The large number of species (ca. 2000), the uncertainty of infrageneric relationships, the reduced reproductive structures, and the existence of many species-level taxonomic problems have hindered efforts to delimit taxa and to understand their phylogenetic relationships (Crins & Ball, 1988; Crins, 1990; Ball & Reznicek, 2002). While recent higher-level phylogenetic studies have provided novel hypotheses regarding infrageneric relationships (Starr et al., 1999, 2004, 2008; Yen & Olmstead, 2000; Roalson et al., 2001), many of the most persistent problems in *Carex* revolve around the circumscription of species and sections (e.g., Reznicek & Ball, 1980; Reznicek, 1986; Crins & Ball, 1988; Naczi, 1992, 2002; Crins & Rettig, 2002; Waterway, 2002). Significant advancements in terms of the discovery of new taxa and in understanding phylogenetic relationships can be achieved through a sectional-level approach to systematics. The reasons for this are many. First, the relatively small size of most sections (< 30 species) allows for the in-depth study of interspecific and intraspecific variation and the resolution of taxonomic problems. Second, the accuracy of results can be practically assessed through the examination of multiple data sets. Third, the phylogenetic position of sections can be determined through a comparison with representatives from putatively related sections. Finally, it allows systematists to relatively easily test the monophyly of sections and clarify sectional limits. As a result of these investigations, sampling strategies can be refined for higher-level phylogenetic studies of both *Carex* and the Cariceae Kunth ex Dumort.

With this philosophy in mind, we have been studying *Carex* sect. *Phyllostachyae* Tuck. ex Kük., a small, well-defined group of woodland carices endemic to North America (see Naczi and Ford [2001] for a discussion of sectional nomenclature). This is one of the most clearly marked groups of sedges, with species characterized by reduced staminate portions of the inflorescences, large, foliaceous pistillate scales, and culms that are strongly dilated at their apices. Several factors favored the selection of section *Phyllostachyae* for our research. These included (1) a clear delimitation from other sections; (2) tractability in terms of number of species and availability of specimens; (3) high levels of intraspecific variation suggesting the presence of additional taxa; and (4) a highly reduced and unusual inflorescence morphology that had led to wide speculation concerning the origin of the section and its systematic position within the genus.

Table 1. Comparison of the taxonomy of *Carex* sect. *Phyllostachyae* in 1992 versus 2008. Question mark indicates the controversial taxonomic status of *C. saximontana* prior to the studies by Starr and Ford (2001) and Saarela and Ford (2001).

1992 (4–5 species)		2008 (10 species)
C. backii *C. saximontana?*	→	*C. backii* Boott in Hook., 1839 *C. saximontana* Mack., 1906 *C. cordillerana* Saarela & B. A. Ford, 2001
C. latebracteata	→	*C. latebracteata* Waterf., 1954
C. jamesii	→	*C. jamesii* Schwein., 1824 *C. juniperorum* Catling, Reznicek & Crins, 1993 *C. timida* Naczi & B. A. Ford, 2001
C. willdenowii	→	*C. willdenowii* Willd., 1805 *C. superata* Naczi, Reznicek & B. A. Ford, 1998 *C. basiantha* Steud., 1855

This paper presents an overview of aspects of our research conducted on section *Phyllostachyae* over the past decade (Ford et al., 1998a, b, c; Naczi et al., 1998; Starr et al., 1999; Ford & Naczi, 2001; Naczi & Ford, 2001; Saarela & Ford, 2001; Starr & Ford, 2001; Starr & Ford, unpubl. data). Here we provide a synopsis of our systematic research highlighting a much larger trend of taxonomic discovery in *Carex*. We also examine the phylogenetic position of section *Phyllostachyae* in the genus and the relationships among its species. Our studies emphasize the benefits of a sectional-level investigation and the advantage of a multidisciplinary approach to systematics studies in sedges.

Taxonomy of *Carex* sect. *Phyllostachyae*

One of the most unexpected findings of our research has been the discovery of a proportionately large number of previously undetected or undescribed species in section *Phyllostachyae*. The number of species now recognized doubled over a

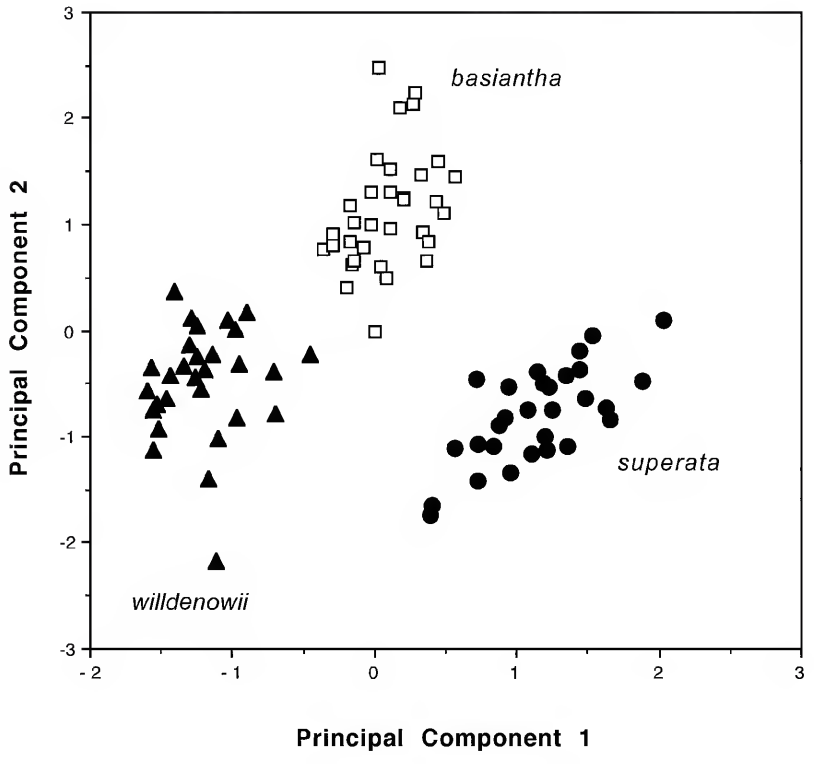

Figure 1. Scatter plot of the scores from Principal Components 1 and 2 for 92 specimens representative of the *Carex willdenowii* complex (Naczi et al., 1998). Reproduced with permission; copyright Botanical Society of America.

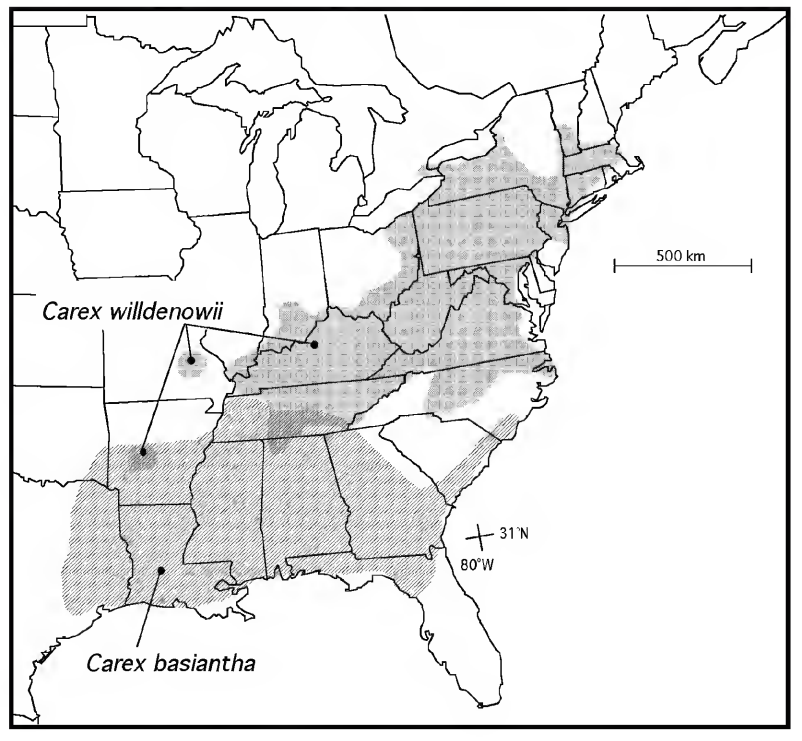

Figure 2. Geographic distribution of *Carex basiantha* and *C. willdenowii* (based on Naczi et al., 1998).

10-year period (Table 1). In all cases these new species turned out to be members of widespread species complexes that were masquerading under a single name (*Carex willdenowii* Willd., *C. jamesii* Schwein., or *C. backii* Boott in Hook.). It was only after the examination of herbarium specimens and extensive fieldwork, especially becoming familiar with regional variation and syntopy of different taxa, that we were alerted to the presence of significant taxonomic variation within each taxon. Macro- and micromorphologic, anatomic, genetic, and phytogeographic data were invaluable in substantiating our taxonomic hypotheses. The following summarizes the findings from our taxonomic investigations.

CAREX WILLDENOWII COMPLEX

Carex willdenowii s.l. is a distinctive taxon that can be distinguished from other species in section *Phyllostachyae* by the combination of nonconcealing, hyaline-margined pistillate scales, perigynia with gradually tapering beaks, obtuse staminate scales, filiform stigmas, and relatively large numbers of staminate flowers. This taxon and *C. jamesii* s.l. make up the narrow-scaled clade of section *Phyllostachyae* (see section entitled "Phylogeny of *Carex* sect. *Phyllostachyae*").

Carex willdenowii s. str. was described very early in the history of North American botanical exploration (Willdenow, 1805), and is a species that is universally recognized in the floras of eastern North America. *Carex basiantha* Steud. (Steudel, 1855) and *C. willdenowii* var. *megarrhyncha* F. J. Herm. (Hermann, 1954), on the other hand, are names that either languished in obscurity as synonyms of *C. willdenowii* (Kükenthal, 1909; Mackenzie, 1935) or were ignored (e.g., Radford et al., 1968; Jones & Coile, 1988; Wofford & Kral, 1993; Smith, 1994). Extensive fieldwork and an examination of herbarium material revealed that these names were in fact correlated with three distinctive morphologies: each found in a particular region of North America and each worthy of recognition at the species level.

A principal components analysis based on eight continuous macromorphologic characters, measured on 92 specimens, along with the construction of voucher-based distribution maps, confirmed our initial observations (Figs. 1–3) (Naczi et al., 1998). *Carex willdenowii* s. str. is widespread across the northeastern United States and is the smallest member of the complex. This sedge is characterized by short staminate portions in the inflorescence (usually 4.9–8.6 mm long), short perigynia (usually 4.5–5.7 mm long), and culms that are on average two thirds the length of plant height. The other two species,

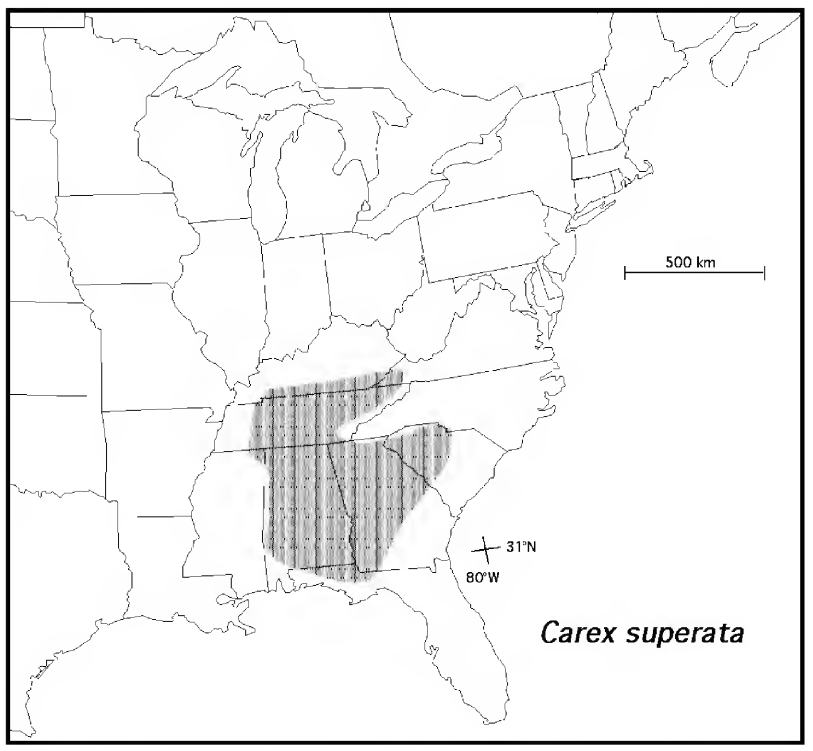

Figure 3. Geographic distribution of *Carex superata* (based on Naczi et al., 1998).

C. basiantha and *C. superata* Naczi, Reznicek & B. A. Ford (= *C. willdenowii* var. *megarrhyncha*), are found in the southeastern and south-central United States and are recognized by their longer staminate portions of terminal spikes (12.7–25.6 mm, 9.6–20.1 mm, respectively) and longer perigynia (5.8–8.0 mm, 7.5–10.8 mm, respectively). *Carex superata* is found in scattered locations throughout the Southeast and is easily distinguished from *C. basiantha* by its short culms, which are greatly exceeded by the foliage, and longer perigynia. In contrast, *C. basiantha* is identified by its tallest culms being on average two thirds the height of the plant and by its shorter perigynia. This species is widespread throughout the southeastern and south-central United States.

A wide body of other evidence also supported the recognition of three species in the *Carex willdenowii* complex. Though few differences could be found in leaf and culm anatomy, distinctive patterns were seen in the silica deposits in achene epidermal cells (Starr & Ford, 2001). In *C. basiantha*, the central platform is ruminate and flat, while in *C. superata* the surface is smooth and rises continuously to the top of the central body (Fig. 4). In contrast, *C. willdenowii* uniquely possesses a central platform with well-developed satellite bodies (Fig. 4).

Isozyme analysis also fully corroborated our morphologic and phytogeographic data (Ford et al., 1998a). A cluster analysis of 14 populations, representing all three species, using Nei's (1978) unbiased genetic identity values, showed the presence of three distinct groups, with a close association evident between *Carex basiantha* and *C. superata* (Fig. 5). Interestingly, this same pattern of relationship was also recovered in a molecular phylogenetic study of section *Phyllostachyae* that showed *C. basiantha* and *C. superata* to be sister species (see section entitled "Phylogeny of *Carex* sect. *Phyllostachyae*").

Ecological trends were also apparent. While all three species inhabit deciduous forests, *Carex basiantha*, *C. superata*, and *C. willdenowii*, respectively, were found to track an environmental gradient related to increasing elevation on slopes and lower pH, moisture, and calcium levels in the soil (Naczi et al., 1998).

The combined evidence from our morphologic, phytogeographic, enzymatic, and ecologic studies clearly supported the recognition of three species in the *Carex willdenowii* complex.

CAREX JAMESII COMPLEX

Since the mid-1980s one of us (RFCN) had been aware of the presence of unusual populations of sedges in the southeastern and central United States that looked similar to *Carex jamesii* but differed in a number of key features. It was not until we had carried out morphologic, phylogenetic, and isozyme studies of section *Phyllostachyae*, and conducted extensive fieldwork throughout the eastern United States that we were able to determine both the taxonomic status of these populations and circumscribe the *C. jamesii* complex (Ford et al., 1998c; Ford & Naczi, 2001; Naczi & Ford, 2001). Based on our findings, the *C. jamesii* complex is composed of three species: *C. jamesii* s. str., *C. juniperorum* Catling, Reznicek & Crins, and *C. timida* Naczi & B. A. Ford. Morphologically and phylogenetically, this complex is closest to the *C. willdenowii* complex, but it can be distinguished by perigynium bodies that are abruptly contracted to beaks and truncate staminate scales. All three species of the *C. jamesii* complex share identical internal transcribed spacer (ITS) sequences (Starr, 1997; Starr et al., 1999; Starr & Ford, unpubl. data).

Principal components analysis based on nine continuous macromorphologic characters measured on 74 specimens, as well as micromorphologic studies, showed the presence of three distinct taxa (Figs.

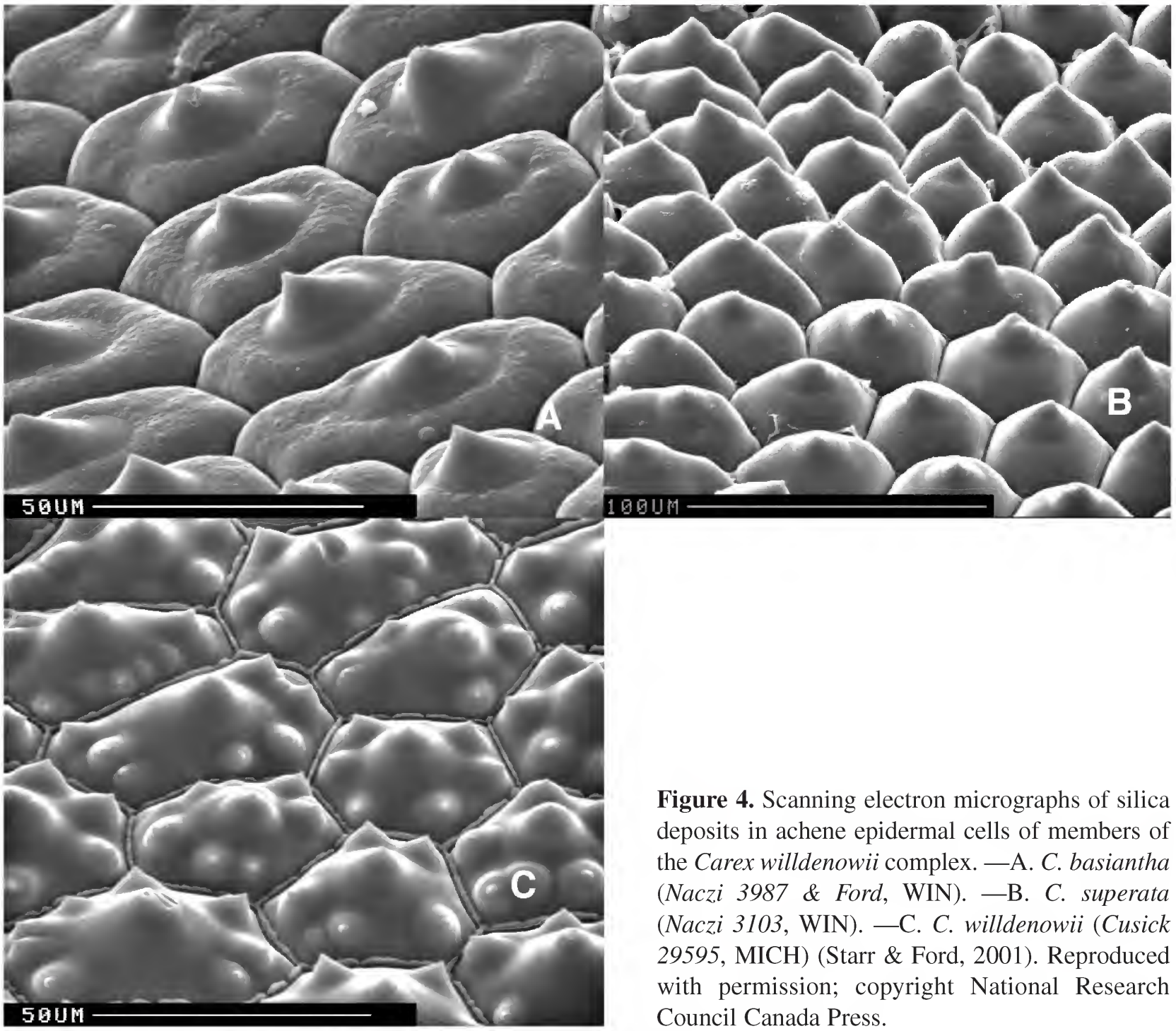

Figure 4. Scanning electron micrographs of silica deposits in achene epidermal cells of members of the *Carex willdenowii* complex. —A. *C. basiantha* (*Naczi 3987 & Ford*, WIN). —B. *C. superata* (*Naczi 3103*, WIN). —C. *C. willdenowii* (*Cusick 29595*, MICH) (Starr & Ford, 2001). Reproduced with permission; copyright National Research Council Canada Press.

6, 7) worthy of recognition at the species level. *Carex juniperorum* is the most divergent member of this complex and is distinguished by its short culms and lack of hyaline margins on the pistillate scales, five or more perigynia in an inflorescence, and red-purple cataphylls with bulging epidermal cells. *Carex jamesii* and *C. timida* possess elongate culms and pistillate scales with conspicuously hyaline margins, and one to three perigynia per inflorescence. Both species are morphologically very similar. However, *C. jamesii* has brown cataphylls with sunken epidermal cells, while the cataphyll morphology in *C. timida* is similar to that found in *C. juniperorum*. In addition, *C. timida* has very short staminate portions to the inflorescence relative to *C. jamesii* (usually 3.4–5.6 mm vs. 5.8–13.5 mm) and longer proximal staminate scales (usually 2.1–3.3 mm vs. 1.1–1.8 mm).

All three species are sympatrically distributed (Figs. 8, 9). *Carex jamesii* is found throughout much of the eastern and central United States and in southern Ontario, Canada. *Carex juniperorum* is much more localized, occurring in three disjunct areas: southeastern Ontario, southwestern Virginia, and the southern Ohio/northeastern Kentucky region. *Carex timida* is known from only 20 counties scattered between southwestern Ohio and easternmost Oklahoma. All three species inhabit mesic, calcareous, deciduous woodlands, with *C. juniperorum* and *C. timida* often found in habitats with a significant red juniper (*Juniperus virginiana* L.) component.

Isozyme data supported the recognition of three species in the *Carex jamesii* complex, although the distinction between species was not as clear as that found in our study of the *C. willdenowii* complex. Furthermore, the relationships implied in the cluster

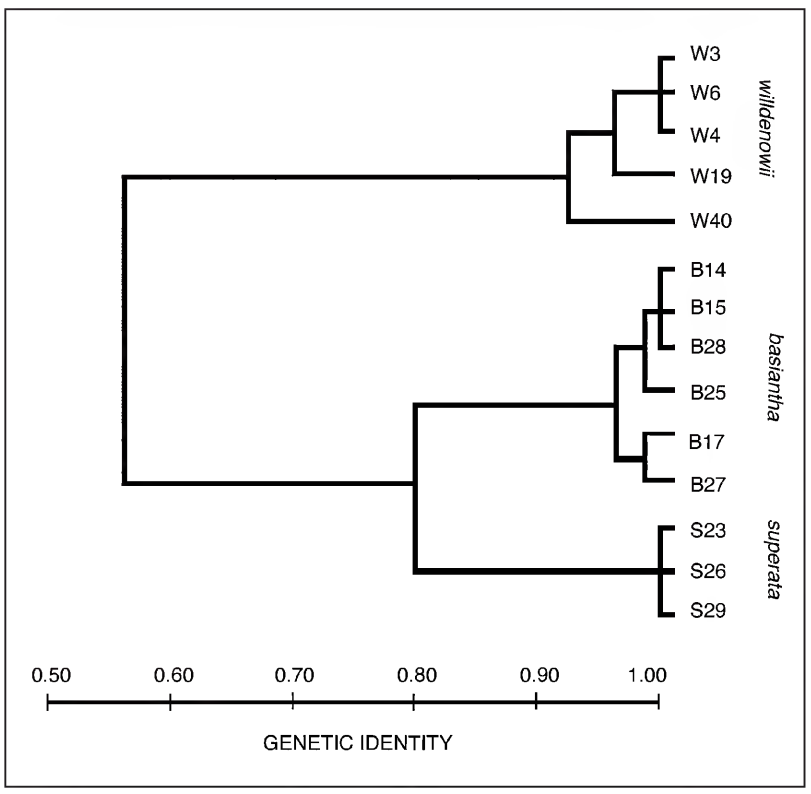

Figure 5. Dendrogram of 14 populations of the *Carex willdenowii* complex using Nei's (1978) unbiased genetic identities and unweighted pair group method with arithmetic averages (UPGMA) cluster analysis (Ford et al., 1998a). Reproduced with permission; copyright Botanical Society of America.

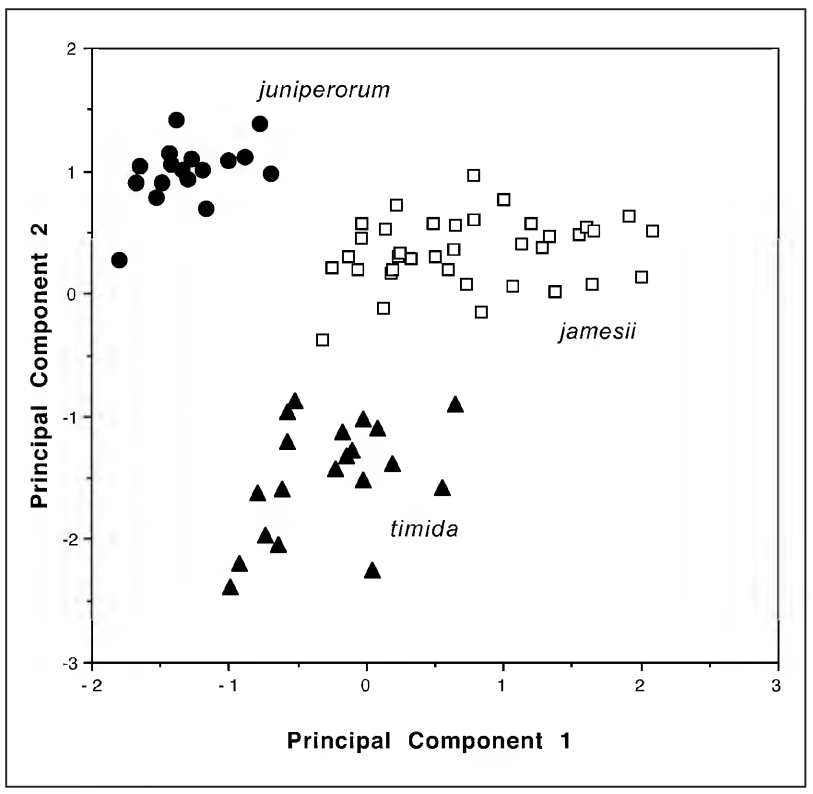

Figure 6. Scatter plot of the scores from Principal Components 1 and 2 for 74 specimens representative of the *Carex jamesii* complex (Naczi & Ford, 2001). Reproduced with permission; copyright Botanical Research Institute of Texas.

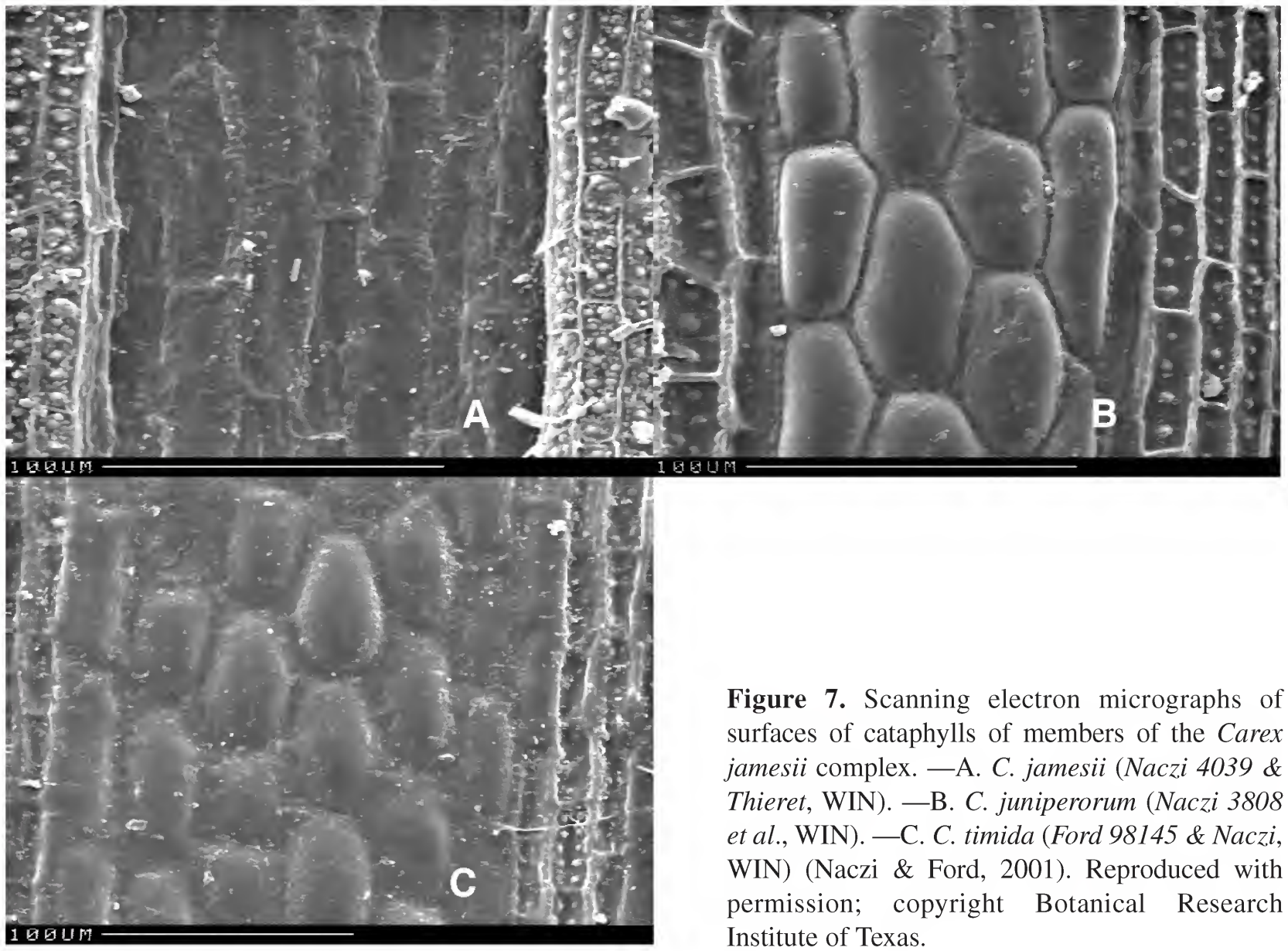

Figure 7. Scanning electron micrographs of surfaces of cataphylls of members of the *Carex jamesii* complex. —A. *C. jamesii* (*Naczi 4039 & Thieret*, WIN). —B. *C. juniperorum* (*Naczi 3808 et al.*, WIN). —C. *C. timida* (*Ford 98145 & Naczi*, WIN) (Naczi & Ford, 2001). Reproduced with permission; copyright Botanical Research Institute of Texas.

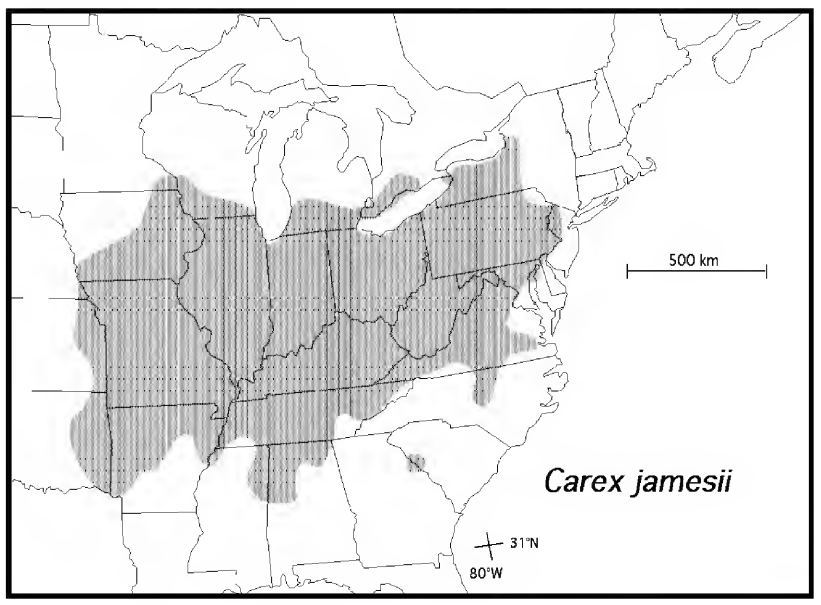

Figure 8. Geographic distribution of *Carex jamesii* (based on Naczi & Ford, 2001).

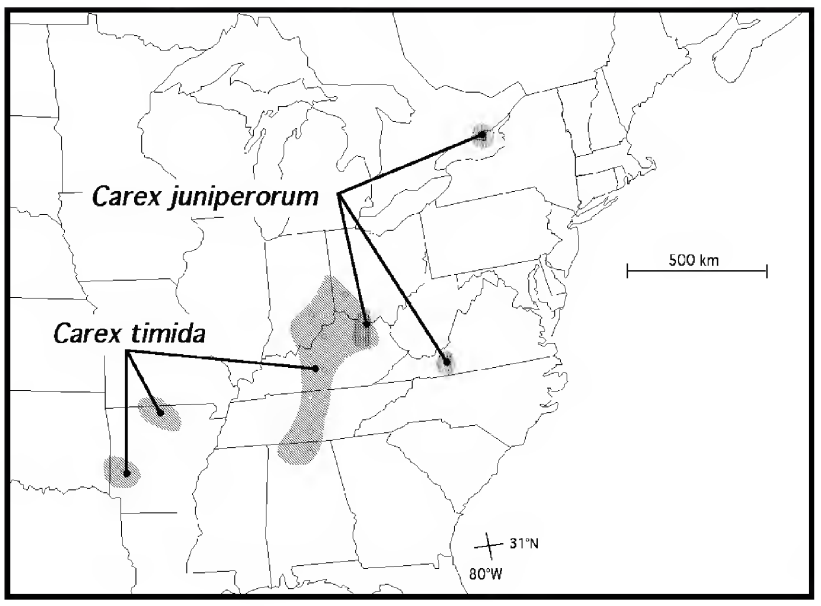

Figure 9. Geographic distribution of *Carex juniperorum* and *C. timida* (based on Naczi & Ford, 2001).

analysis of these data were not those intuitively expected based on our morphologic observations. For example, *C. jamesii* and *C. timida* were clearly separated from one another, despite their morphologic similarity (Fig. 10). On the other hand, *C. timida* and *C. juniperorum*, which are highly distinctive morphologically, were shown to be genetically similar. Interestingly, this close association is congruous with our phylogenetic studies (Naczi & Ford, 2001; see section entitled: "Phylogeny of *Carex* sect. *Phyllostachyae*") that showed *C. juniperorum* and *C. timida* to be sister species. Populations from the Ouachita Mountains of Arkansas, which are genetically intermediate between the two species (populations 16 and 20, Fig. 10), were intriguing because morphologically these plants are clearly *C. timida*. These intermediate populations suggest that *C. timida* and *C. juniperorum* may have originated in the Ouachita Mountains. Alternatively, *C. juniperorum* may have originated from populations or a population of *C. timida* similar to those found in western Arkansas.

As was found in our study of *Carex willdenowii* s.l., micro- and macromorphologic characters, along with phytogeographic and isozyme data, supported the recognition of three species in the *C. jamesii* complex.

CAREX BACKII COMPLEX

Carex backii s.l. (*C. backii* s. str., *C. saximontana* Mack., and *C. cordillerana* Saarela & B. A. Ford = the wide-scaled clade—see section entitled "Phylogeny of *Carex* sect. *Phyllostachyae*") is a distinctive taxon that can be distinguished from other species in the section by a combination of characters, including thick stigmas, wide pistillate scales that conceal the perigynia, and extremely short staminate portions of the inflorescences. This species complex has had a rather checkered taxonomic past with various opinions expressed regarding both the number and rank of the taxa within this group. While some authors have chosen to recognize a single polymorphic species (*C. backii* s.l.), others recognize plants from the Great Plains as being distinct from *C. backii* s. str. [*C. saximontana* = *C. backii* var. *subrostrata* (Bates) Dorn]. Our research revealed that *C. backii* and *C. saximontana* are distinct species and that variability within *C. saximontana* includes a third taxon (*C. cordillerana*) (Saarela & Ford, 2001; Starr & Ford, 2001).

A discriminant functions analysis based on nine continuous macromorphologic characters measured on 79 specimens, along with anatomic, micromorphologic, and phytogeographic data, clearly showed the presence of three species within the *Carex backii* complex (Figs. 11–16). *Carex backii* s. str. is the most distinctive taxon in this group and is easily identified by its long perigynia (4.8–6.6 mm) with smooth surfaces, and long, smooth beaks (1.9–2.9 mm). Marginal sclerenchyma deposits, confined to the adaxial surface of the leaf, are also diagnostic. This is the most widely distributed species in the *C. backii* complex and is found throughout temperate and boreal regions of Canada and the adjacent United States, with disjunct populations found in western North America as far south as Colorado.

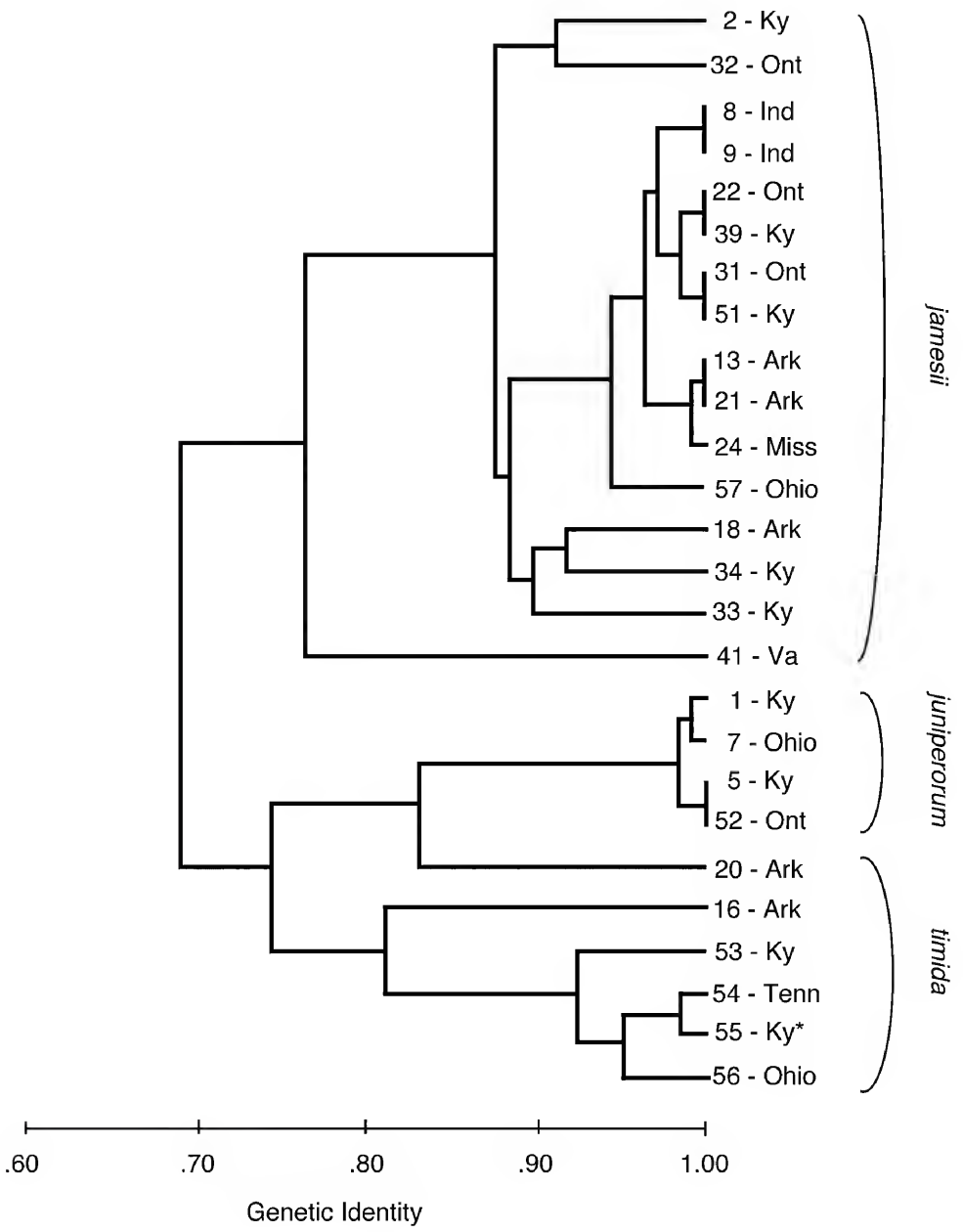

Figure 10. Dendrogram of 26 populations of the *Carex jamesii* complex using Nei's (1978) unbiased genetic identity values and UPGMA cluster analysis (Ford & Naczi, 2001). Reproduced with permission; copyright Botanical Research Institute of Texas.

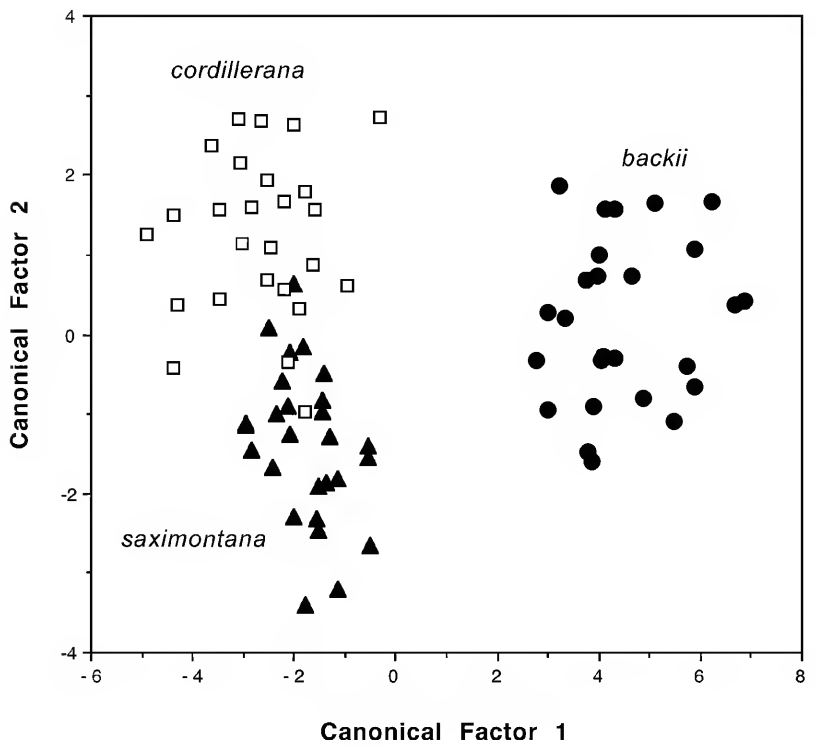

Figure 11. Scatter plot of the scores from Canonical Variates 1 and 2 for 79 specimens representative of the *Carex backii* complex (Saarela & Ford, 2001).

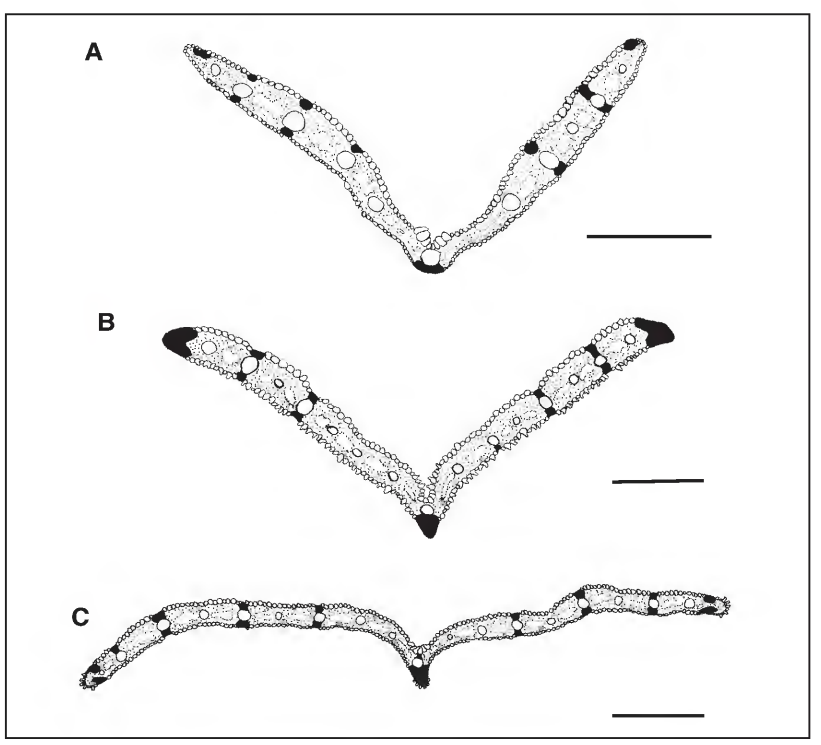

Figure 12. Leaf cross sections. —A. *Carex backii* (*Ford et al. 94191*, WIN). — B. *C. saximontana* (*Ford 9526 & Starr*, WIN). — C. *C. cordillerana* (*Crofts 91-108*, WS). Scale bars represent 0.5 mm. Darkened areas = sclerenchyma, stippled areas = chlorenchyma, stipple-bordered ellipses = air cavities, continuous circles between upper and lower surfaces = vascular bundles (Saarela & Ford, 2001).

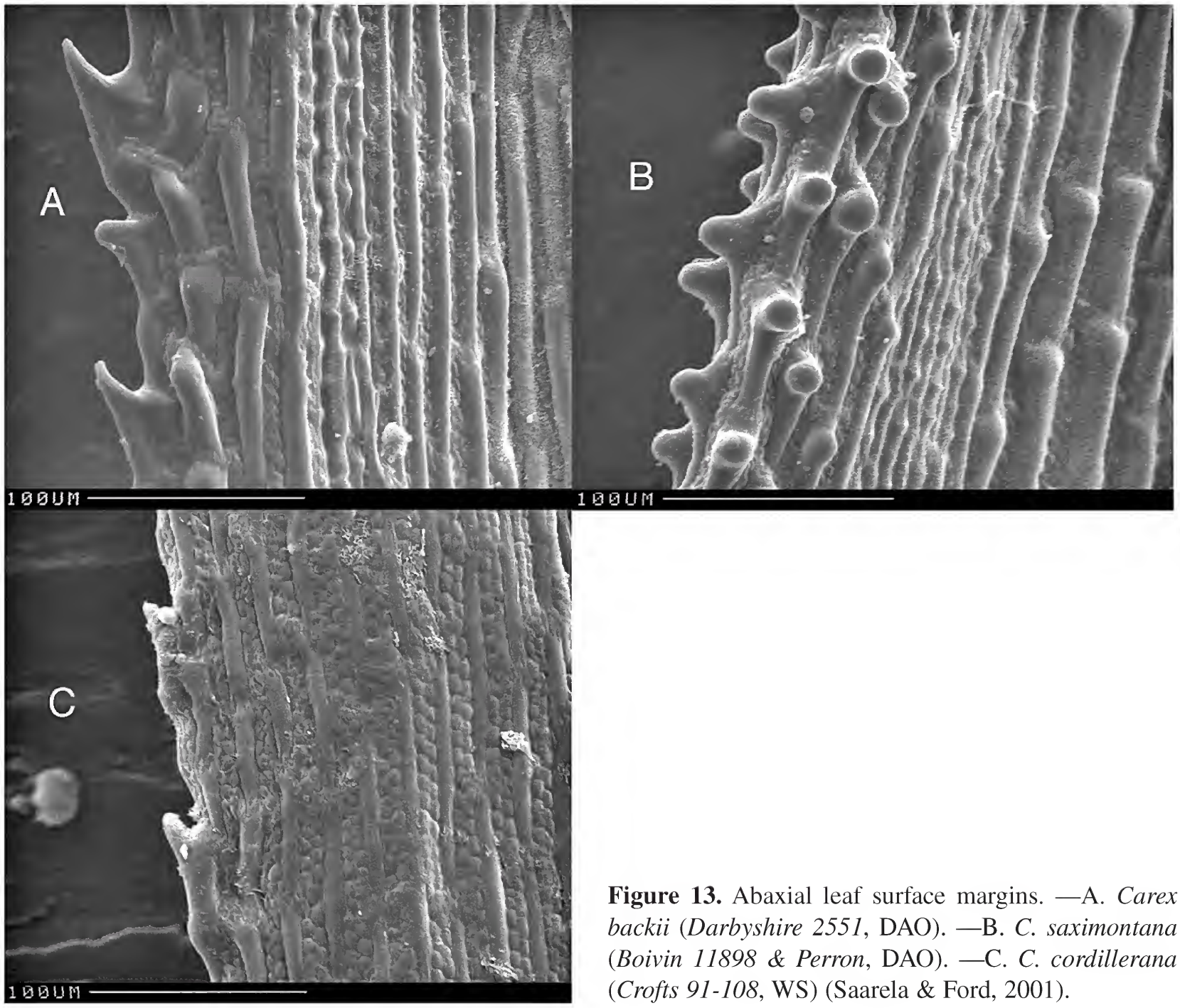

Figure 13. Abaxial leaf surface margins. —A. *Carex backii* (*Darbyshire 2551*, DAO). —B. *C. saximontana* (*Boivin 11898 & Perron*, DAO). —C. *C. cordillerana* (*Crofts 91-108*, WS) (Saarela & Ford, 2001).

Carex saximontana and *C. cordillerana* overlap in all quantitative characters measured, and as a result were incompletely separated in the discriminant functions analysis (Fig. 11). However, anatomic, micromorphologic, and phytogeographic characters show a number of discontinuities supporting the recognition of these taxa at the species level (Figs. 12–14, 16). *Carex saximontana* is restricted to the Great Plains region of North America and is distinguished by its papillose perigynia and leaves that are greenish glaucous to dark herbage green (as described using the color charts of Rayner, 1970) with completely sclerified, hyaline margins. *Carex cordillerana*, on the other hand, has dull green to yellow-green leaves with green, densely papillate leaf margins that have sclerenchyma deposits found adjacent to the adaxial and abaxial surfaces. The perigynium surface appears smooth when examined with a dissecting microscope. However, the epidermal cells have a distinctive convex morphology when viewed under higher magnification. *Carex cordillerana* is completely allopatric with *C. saximontana* and occurs from central British Columbia to northern Utah.

Isozyme studies have demonstrated that *Carex backii* and *C. saximontana* are distinct species despite the fact that they often occur together in mixed populations (see Ford et al., 1998c). Isozyme variation has not been examined in *C. cordillerana*. However, molecular phylogenetic studies have shown that this species, as well as others in the section, can be distinguished by one or more autapomorphies (see section entitled "Phylogeny of *Carex* sect. *Phyllostachyae*").

The combined evidence demonstrated that *Carex backii* s.l. is composed of three distinct species. As with the other complexes previously

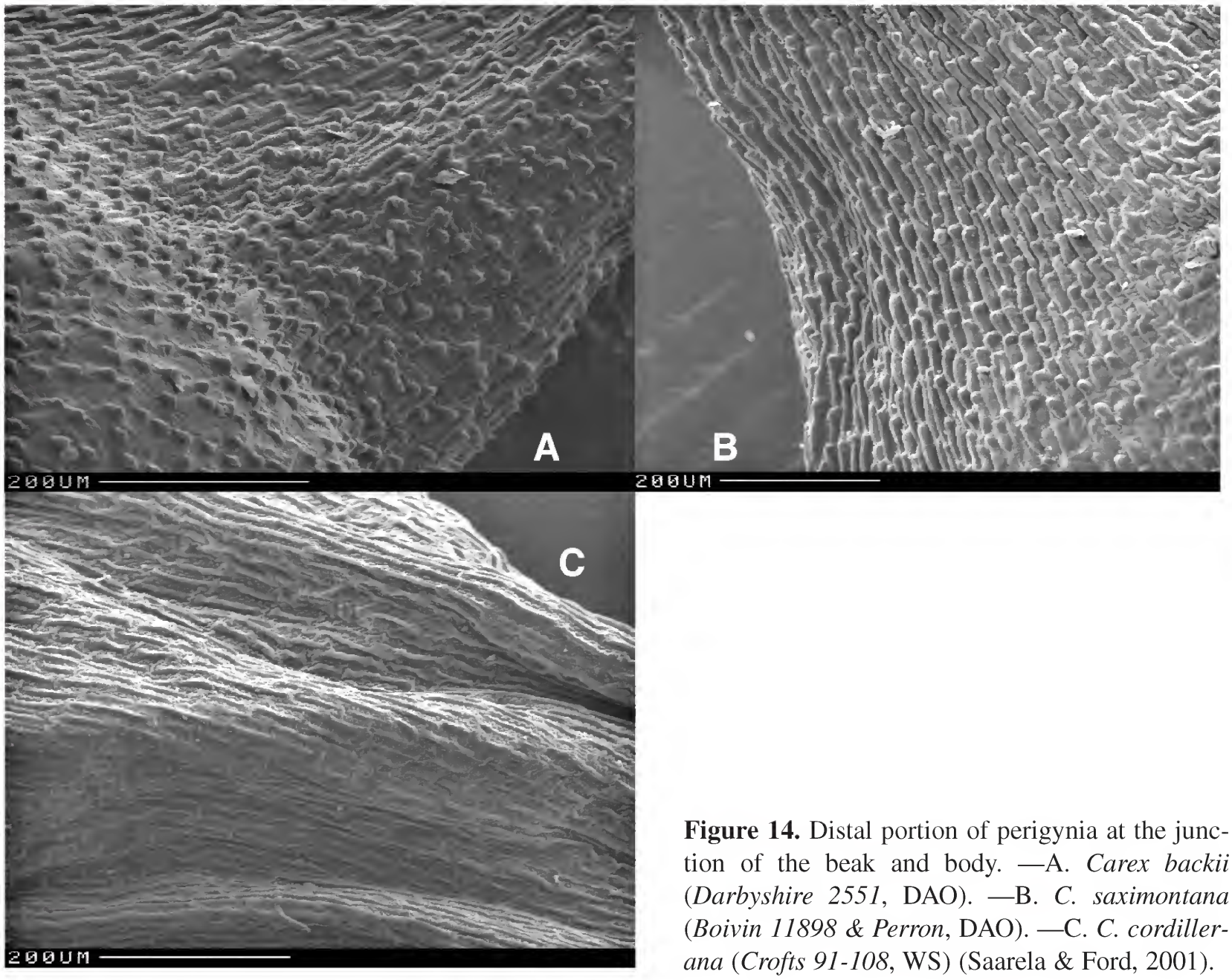

Figure 14. Distal portion of perigynia at the junction of the beak and body. —A. *Carex backii* (*Darbyshire 2551*, DAO). —B. *C. saximontana* (*Boivin 11898 & Perron*, DAO). —C. *C. cordillerana* (*Crofts 91-108*, WS) (Saarela & Ford, 2001).

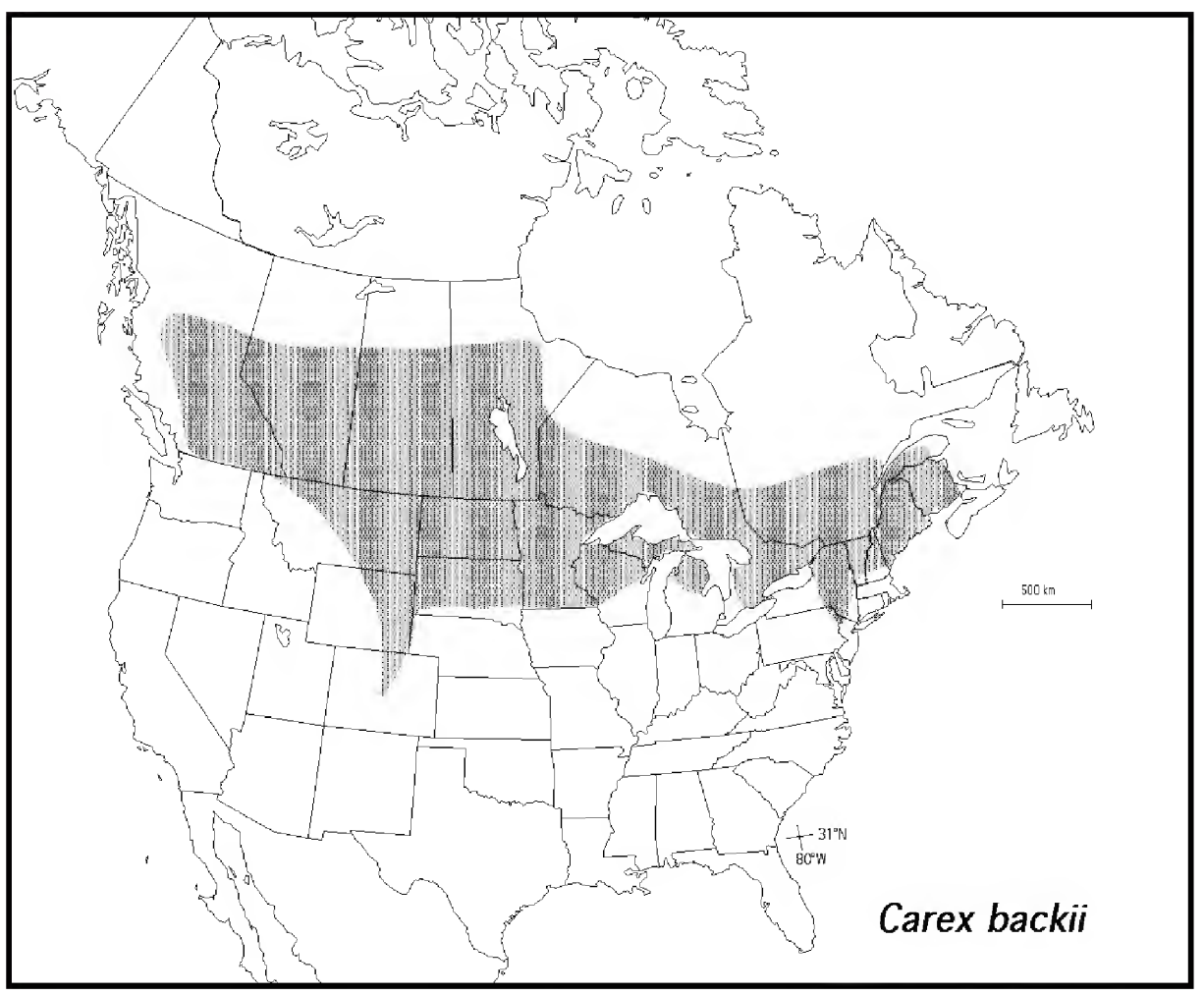

Figure 15. Geographic distribution of *Carex backii* (Saarela & Ford, 2001).

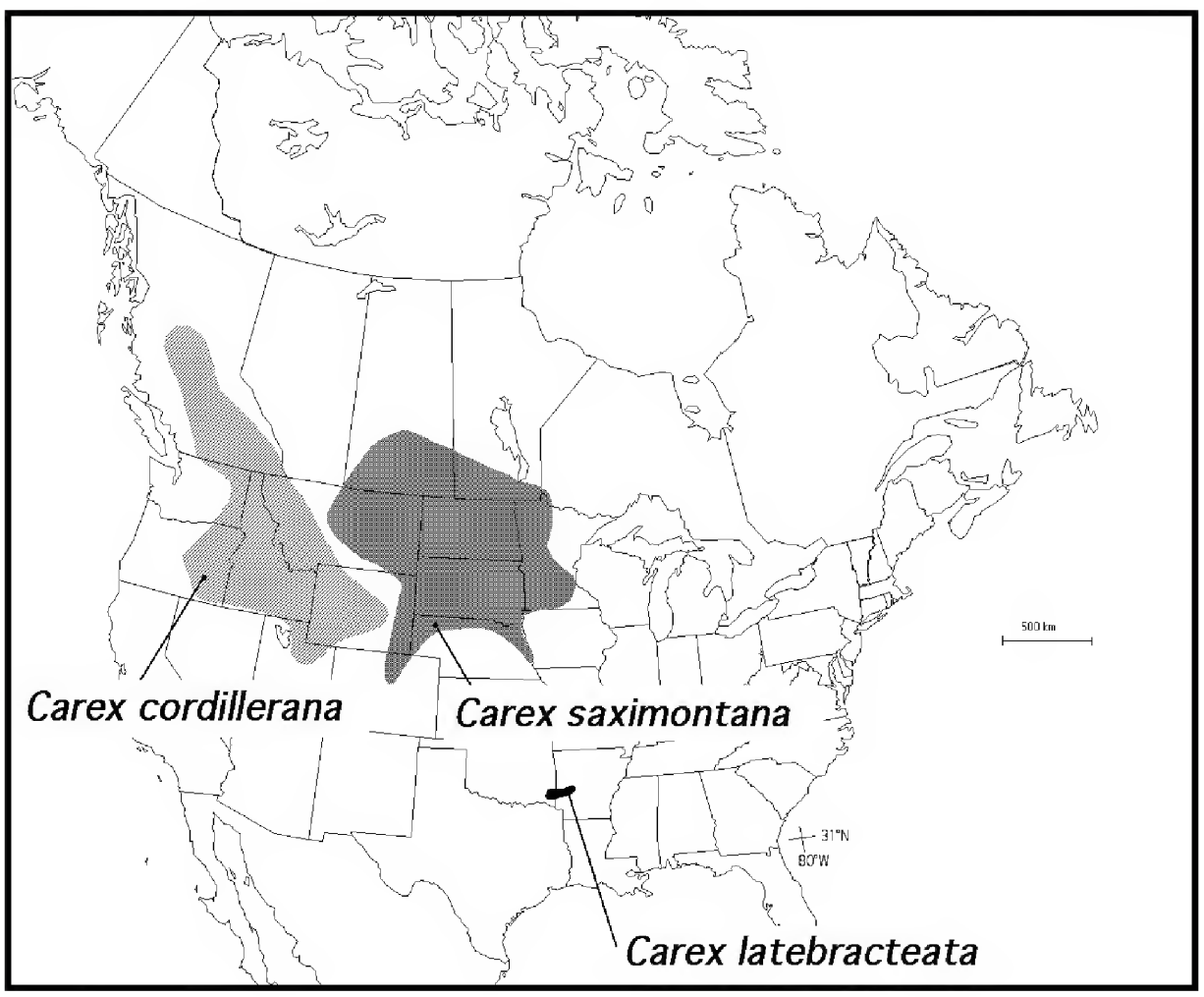

Figure 16. Geographic distribution of *Carex saximontana*, *C. cordillerana*, and *C. latebracteata* (Saarela & Ford, 2001).

described, this study has shown the value of delineating taxa through the integration of evidence from macromorphology, micromorphology, anatomy, phytogeography, and genetics.

CAREX LATEBRACTEATA

Carex latebracteata Waterf. is a narrow endemic from the Ouachita Mountains of Arkansas and eastern Oklahoma (Fig. 16) and is the only species in section *Phyllostachyae* that was found to contain no "hidden" taxa (Naczi & Ford, unpubl. data). *Carex latebracteata* is one of the most distinctive species in the genus. In the field it looks superficially more like an *Iris* L. than a *Carex*! Surprisingly, this species escaped detection until the 1950s when it was first described by Waterfall (1954). *Carex latebracteata* shares a number of features with *C. backii* and its allies (thickened stigmas, wide pistillate scales that conceal the perigynia, and extremely short staminate portions of the inflorescences) but is easily distinguished by its taller stature, much longer perigynia, absence of lateral spikes, and tightly coiled stigmas. Achene silica bodies that possess convex versus concave platforms and persistent outer periclinal walls are also diagnostic (Starr & Ford, 2001) (Fig. 17).

Until recently, we regarded *Carex latebracteata* as part of the wide-scaled clade but now understand that this clade includes only *C. backii* and its allies. *Carex latebracteata* is likely primitive within the section and sister to both the wide- and narrow-scaled clades (see section entitled "Phylogeny of *Carex* sect. *Phyllostachyae*"). A synopsis of the revised taxonomy of *Carex* sect. *Phyllostachyae*, including a key to all its species, appears in Crins et al. (2002).

Taxonomic Conclusions

Our taxonomic work on *Carex* sect. *Phyllostachyae* highlights two important points with respect to systematics work on *Carex*.

1. *The* Carex *flora of North America is not fully known.* The discovery of new species in *Carex* sect. *Phyllostachyae* is part of a larger trend of taxonomic discovery in *Carex* in general. On average two new taxa of *Carex* per year over the past 20 years have been described from North America: the vast majority of these being from the southeastern United States and western North America (Hartman & Nelson, 1998; Naczi et al., 1998, 2002; Ertter, 2000; Saarela & Ford, 2001). In recent years the rate of dis-

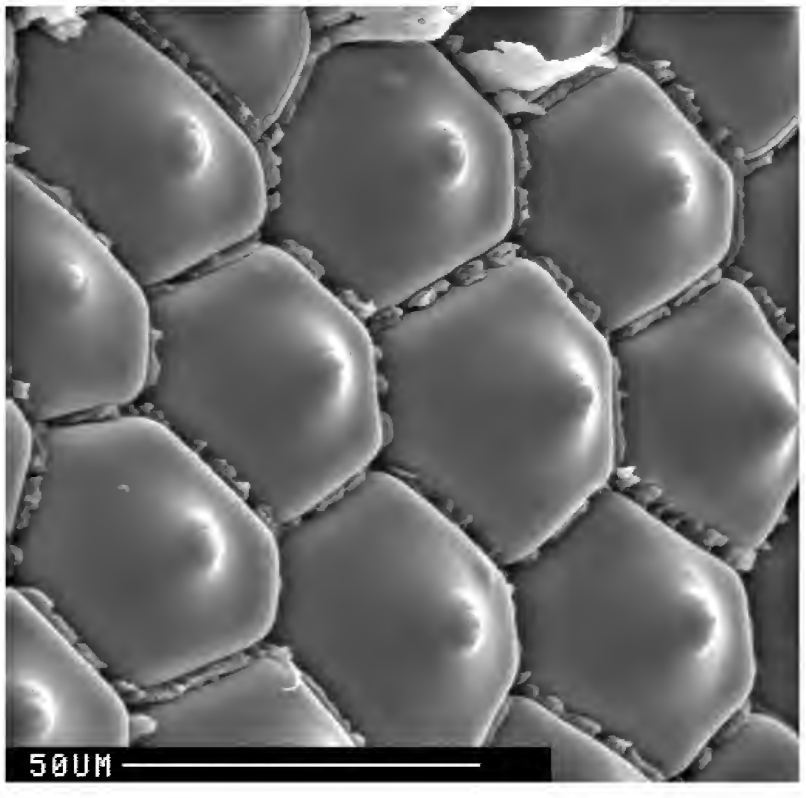

Figure 17. Scanning electron micrographs of silica deposits in achene epidermal cells of *Carex latebracteata* (*Naczi 3953 & Ford*, WIN).

covery has been even more dramatic. Twelve taxa were formally described in North American *Carex* between 2001 and 2002 (Naczi & Ford, unpubl. data). We predict that southeastern and western North America will continue to yield a proportionately large number of new sedge taxa. In particular, collections from known areas of endemism such as the Klamath (sensu Smith & Sawyer, 1988), Cascades, Sierra Nevada, Blue Ridge, and Ouachita Mountains, and the Queen Charlotte Islands should be carefully examined and compared with specimens from elsewhere in North America. Clearly the answer to such a basic question as "How many species of *Carex* occur in North America?" is far from answered.

2. *A multidisciplinary approach is critical in taxonomic studies of* Carex. The parsing of species diversity in section *Phyllostachyae* has not been a straightforward process involving the discovery of overtly distinct taxa in the field. Rather our "wholesale rethinking of the existing taxonomic framework" (Ertter, 2000: 95) has been a gradual process involving the comparison and analysis of existing specimens using a variety of data sources. Field observations, analyses of live material, and phytogeographic studies have been critical to our research.

Phylogeny of *Carex* sect. *Phyllostachyae*

Molecular phylogenetic studies of *Carex* and the Cariceae by Starr et al. (1999, 2004, 2008), Yen and Olmstead (2000), and Roalson et al. (2001) have revolutionized our ideas regarding the evolution of *Carex*. These studies, while different in some aspects, show that all the genera within the Cariceae must be included within a more broadly circumscribed *Carex*. Within this more widely defined view of the genus, three main clades can be distinguished: (1) a compound clade, comprised largely of multispicate species traditionally placed in subgenus *Vigneastra* (Tuck.) Kük. [= *Indocarex* (Baill.) Kük. in Engl.], *Psyllophora* (Degl.) Peterm. (= *Primocarex* Kük in Engl.), and a portion of subgenus *Carex*; (2) a reduced clade made up predominantly of unispicate species traditionally placed in part of subgenus *Carex*, *Psyllophora*, plus all other genera in the Cariceae (*Cymophyllus* Mack., *Kobresia* Willd., *Uncinia* Pers., *Schoenoxiphium* Nees); and (3) subgenus *Vignea* (P. Beauv. ex T. Lestib.) Peterm. Sequence data from the ITS and external transcribed spacer (ETS) regions of nuclear ribosomal DNA (nrDNA) (ITS-1, ITS-2, ETS 1f) showed *Carex* sect. *Phyllostachyae* to be monophyletic and part of the reduced clade (Starr et al., 1999, 2004, 2008) with unispicate species in *Carex* sections *Firmiculmes* Kük. and *Filifoliae* (Tuck.) Mack., and *Cymophyllus fraserianus* (Ker Gawl.) Kartesz & Gandhi being sister to the *Phyllostachyae* (Starr et al., 1999, 2008; Starr & Ford, unpubl. data).

While phylogenetic relationships within section *Phyllostachyae* were explored by Starr et al. (1999), patterns of relationships were not fully resolved because of the limited data set (ITS data only). The research presented here incorporates both ITS and ETS 1f sequence data plus a suite of 20 morphologic characters. For our study we included all 10 species from section *Phyllostachyae* plus three outgroup taxa: *Carex filifolia* Nutt. (sect. *Filifoliae*), *C. geyeri* Boott (sect. *Firmiculmes*), and *Cymophyllus fraserianus*. Outgroup taxa were chosen on the basis of previous studies that had hypothesized that these species might be closely related to section *Phyllostachyae* (Starr et al., 1999, 2004, 2008; Starr & Ford, unpubl. data).

Maximum parsimony analysis yielded two most parsimonious trees with the strict consensus shown in Figure 18. The same topology is also recovered

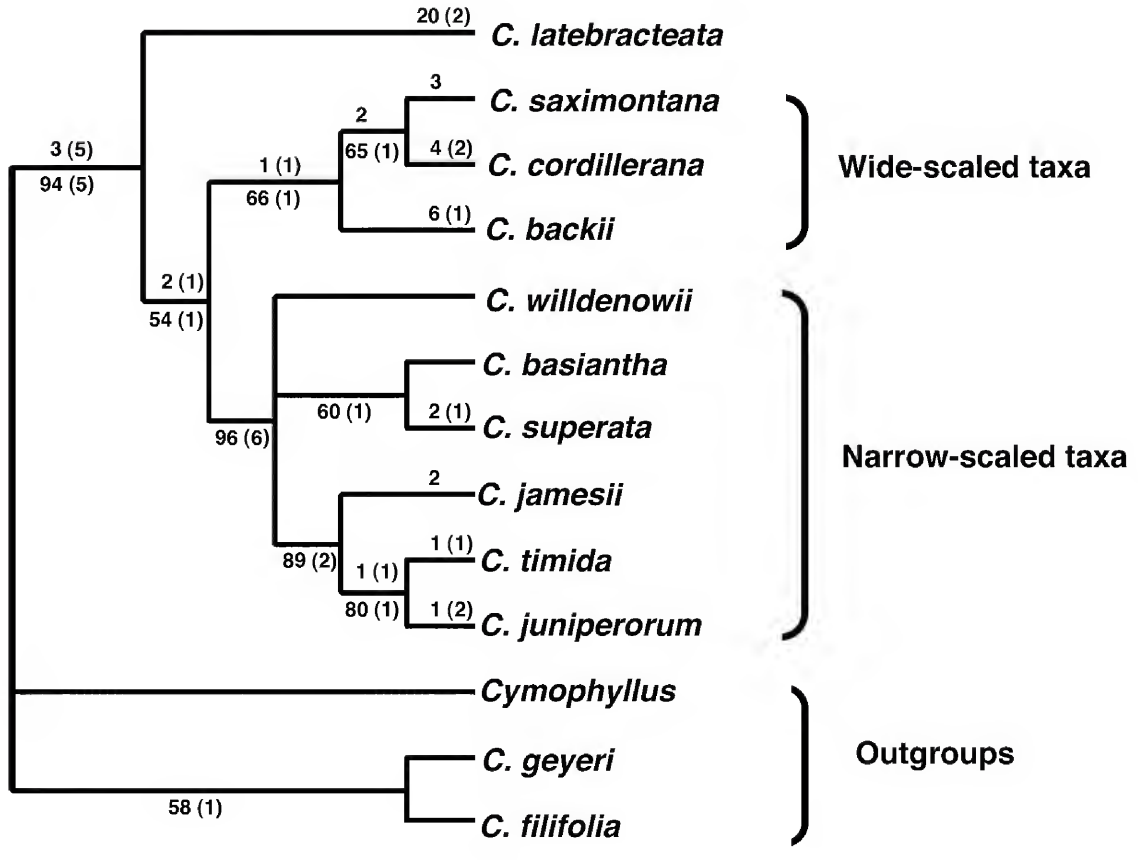

Figure 18. The strict consensus of two most parsimonious trees resulting from the phylogenetic analysis of *Carex* sect. *Phyllostachyae* using ITS, ETS 1f, and morphological data. Bootstrap and decay indices (in parentheses) are given below the branch. Molecular and morphological (in parentheses) apomorphies for the ingroup are given above the branch. Consistency index (CI) excluding uninformative characters = 0.65, retention index (RI) = 0.68.

using maximum likelihood. Analyses that excluded the morphologic data yielded identical results to a study based entirely on the combined data set (Starr & Ford, unpubl. data).

Our findings indicate that section *Phyllostachyae* is composed of three monophyletic groups. The narrow-scaled clade (*Carex basiantha*, *C. jamesii*, *C. juniperorum*, *C. superata*, *C. timida*, *C. willdenowii*) is characterized by scales that do not conceal the perigynia, filiform stigmas, and relatively large numbers of staminate flowers. In contrast, species in the wide-scaled clade (*C. backii*, *C. cordillerana*, *C. saximontana*) are distinguished by pistillate scales that conceal the perigynia, thick stigmas, and relatively small numbers of staminate flowers. *Carex latebracteata* is sister to both the wide- and narrow-scaled clades. Interestingly, it is not closely related to the members of the *C. backii* complex with which it had been previously associated (see Ford et al., 1998c). However, this relationship is consistent with the macro- and micromorphologic differences that have been noted in this taxon (see above). Bootstrap and decay values indicate at least moderate support for most clades, with the narrow-scaled clade and the *C. jamesii* complex having the highest values.

The relationships shown within the various species complexes are comparable to those hypothesized in previous isozyme studies (see Ford et al., 1998a, c; Ford & Naczi, 2001) and cladistic analysis of molecular and morphologic data (Starr et al., 1999; Naczi & Ford, 2001). However, a couple of these relationships are worth commenting on further. *Carex willdenowii* remains an enigmatic taxon whose relationship is still unclear. The equivocal positioning of *C. willdenowii* was evident in a previous isozyme study of the section (see Ford et al., 1998c) and in the molecular phylogeny presented here. The combined evidence suggests that even if the *C. willdenowii* complex is monophyletic, *C. willdenowii* is highly divergent from both *C. basiantha* and *C. superata*.

A previous phylogenetic analysis of the *Carex jamesii* complex based on 13 morphologic characters supported the sister-group relationship for *C. juniperorum* and *C. timida* (Naczi & Ford, 2001). Our molecular phylogeny provides strong independent support for this relationship.

A previous isozyme study of the *Carex backii* complex did not include *C. cordillerana* in the analysis. Our results indicate that the *C. backii* complex is monophyletic and that *C. saximontana* and *C. cordillerana* are sister species. The close relationship between the latter two species is not unexpected since these two species have been shown to be close phenetically. Most herbarium collections of *C. cordillerana* were originally identified as *C. saximontana*.

While molecular data are most often used for phylogenetic studies, it is important to note that most species are characterized by at least one molecular autapomorphy (Starr et al., 1999, 2008; Starr & Ford, unpubl. data). Thus, molecular data provided further evidence in support of our revised taxonomy of this section.

Future Research on *Carex* sect. *Phyllostachyae*

While section *Phyllostachyae* has become one of the most studied sections of *Carex*, there are a number of opportunities for future research.

Quantitative ecological studies of this section have not been conducted but could provide insights into niche partitioning in *Carex* and a better understanding of evolutionary processes in sympatric anemophilous species. Studies such as that by Bayer et al. (1991) could serve as an example for such research.

Chromosome number variation has been studied extensively in many *Carex* sections, with chromosome number known to vary between species within a section, populations within a species, and even between individuals within a population (see references cited in Naczi, 1999). While chromosome number may vary randomly within a species or species complex, it is often correlated with the macromorphologic characters used to delimit morphologically similar taxa (see Naczi, 1992). There may also be a correlation between geographic distribution, ecology, and/or phylogenetic relatedness (see Crins & Ball, 1988; Crins, 1990; Naczi, 1992, 1999; Hoshino & Okamura, 1994; Hoshino & Waterway, 1994). Chromosome numbers are known for half the species in section *Phyllostachyae* (*C. willdenowii*: $2n = 62, 78$; *C. jamesii*: $2n = 66, 70$; *C. saximontana*: $2n = 64$; *C. backii*: $2n = 66$; *C. latebracteata*: $2n = 98$; Crins et al., 2002). While chromosome number appears to have no correlation with phylogenetic relationships in section *Phyllostachyae*, trends related to interspecific variation (especially in taxa such as *C. jamesii*), species distribution, and ecology may be present.

Phylogeographic studies (see Avise, 2000) have not been conducted on any group of sedges to date. Localized endemics such as *Carex latebracteata*, which is confined to river and stream systems in the Ouachita Mountains of Arkansas and Oklahoma, are ideally suited to the study of the geographic distribution of lineages within a species.

Conclusions

Our studies of *Carex* sect. *Phyllostachyae* have allowed us to gain insights into the systematics of this taxon. Our findings also have wider implications in terms of future directions for systematics studies of the genus. Our research suggests the following:

1. *Species diversity in many* Carex *sections is greater than previously realized.* We suspect that section *Phyllostachyae* is just the tip of the iceberg. Other sections in North America may prove, or have proven, to be rich sources of taxonomic novelties. These include sections *Acrocystis* Dumort., *Careyanae* Tuck. ex Kük., *Griseae* (L. H. Bailey) Kük., *Laxiflorae* (Kunth) Mack., and *Ovales* Kunth. Regions such as temperate South America and eastern Asia, which are also known to have diverse sedge floras, probably represent even greater potential for previously unsuspected diversity. Integrating numerous sources of evidence (macromorphology, micromorphology, anatomy, phytogeography, molecular) will be critical to resolving many of these taxonomically complex sections and understanding the *Carex* flora in various regions of the globe.

2. *A detailed phylogeny of* Carex *at the sectional level is an attainable goal.* Indeed, efforts toward the completion of this task have already taken place (e.g., Ford et al., 2006; Waterway & Starr, 2007). A concerted effort among caricologists focused on phylogenetic reconstruction using nrDNA and chloroplast DNA (cpDNA) markers will allow for a detailed picture of evolutionary relationships.

These two avenues of research represent the overarching initiatives of most systematics research: the parsing of taxonomic diversity and understanding phylogenetic relationships. *Carex* serves as a striking reminder of the necessity for both avenues of research in understanding global biodiversity.

Acknowledgments

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Research Council of Canada (NSERC) Discovery Grant to BAF.

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Chapter 12

Phylogeny of the Unispicate Taxa in Cyperaceae Tribe Cariceae II: The Limits of *Uncinia*

Julian R. Starr, Stephen A. Harris, and David A. Simpson

ABSTRACT Debates on the limits and relationships of Cariceae genera and subgenera have historically focused on a small number of unusual "transitional" taxa and on scenarios involving a reduction or proliferation of rachillae (i.e., spikelet secondary axes). The strongest argument for such theories was provided by *Carex microglochin* Wahlenb. and *Uncinia kingii* Boott, a seemingly indisputable link between *Carex* L. and *Uncinia* Pers. In this study we examine the limits of *Uncinia* by focusing on these transitional species and their allies in *Carex* subg. *Psyllophora* (Degl.) Peterm., a reduced unispicate group whose species are largely responsible for blurring generic and *Carex* subgeneric limits. Phylogenies derived from ITS and ETS 1f sequences representing 72 taxa and all five Cariceae genera distinguished four major clades (A, B, C, D), including a predominately unispicate, androgynous clade (A and B) that rejects the classic *U. kingii*/*C. microglochin* transition series (i.e., they are polyphyletic). Nonetheless, analyses strongly support a sister relationship between *Uncinia* s. str. and *U. kingii*. This is an unexpected result, for strong anatomical and morphological evidence would suggest that *U. kingii* is closest to *C. microglochin* and its allies. Moreover, the sister position of *U. kingii* to *Uncinia* s. str. suggests that contrary to previous classifications of *Uncinia* the characters of *Uncinia* sect. *Uncinia* are plesiomorphic. This means that despite section *Uncinia* being largely natural in this analysis, it—like *Uncinia* s.l.—cannot be defined by any known morphological apomorphy. The implications of the analysis for generic and *Carex* subgeneric relationships, including the subgeneric and sectional classification of *Uncinia*, are discussed.

KEY WORDS *Carex microglochin*, Cariceae phylogeny, ETS 1f, generic circumscription, ITS, *Uncinia* classification, *Uncinia kingii*.

The tribe Cariceae Kunth ex Dumort. (ca. 2100 spp.) comprises nearly half of all the species found in the large and taxonomically complex Cyperaceae (Reznicek, 1990). It is a cosmopolitan tribe of herbaceous, predominately anemophilous perennials that occur in diverse habitats ranging from rainforests to tundra. The group is readily marked within the family by the combination of two distinctive features: strictly unisexual flowers and a utricle or perigynium, which is a flask-shaped prophyll that surrounds the naked gynoecium (Blaser, 1944). These uncommon characters clearly discriminate the group, and its circumscription has rarely been debated.

In contrast, the limits and relationships of the tribe's five principal genera (*Carex* L., *Cymophyllus* Mack., *Kobresia* Willd., *Schoenoxiphium* Nees, *Uncinia* Pers.; Reznicek, 1990) are highly controversial (Fig. 1). This is largely due to the numerous taxonomic problems that surround the genus *Carex* (2000 spp.), one of the most widespread and ecologically significant angiosperm genera (Reznicek, 1990). *Carex* exhibits a considerable amount of variation in the structure of its inflorescence (Fig. 2), ranging from the multispicate species in *Carex* subgenera *Carex* p.p., *Vigneastra* (Tuck.) Kük. [= *Indocarex* (Baill.) Kük.], and *Vignea* (P. Beauv. ex T. Lestib.) Peterm. p.p. that may resemble elements in the genera *Schoenoxiphium* or *Kobresia* p.p., to the extremely reduced, unispicate species of *Carex* subg. *Psyllophora* (Degl.) Peterm. [= *Primocarex* Kük.] and *Carex* p.p. that are reminiscent of the genus *Uncinia* or reduced *Kobresia* species. This wide range in the number of flowers and in the structural complexity of the inflorescence has given rise to a long history of tribal classification schemes that are based on evolutionary scenarios involving a small number of "phylogenetic" characters (Kükenthal, 1909; Kreczetovicz, 1936; Nelmes, 1951, 1952; Savile & Calder, 1953), phytogeographical arguments (Kükenthal, 1909; Nelmes, 1951, 1952), and a collection of unusual species that appear to transgress generic limits (e.g., Kükenthal, 1909, 1940; Kreczetovicz, 1936; Ivanova, 1939; Nelmes, 1952).

Historically, the most important characters for generic and subgeneric circumscription have been the gross morphology of the inflorescence (unispicate vs. multispicate), the distribution of the sexes in spikelets (bisexual vs. unisexual), and the degree of fusion of the utricle (open vs. closed to apex) (Fig. 1). These three characters apparently separated the species of *Kobresia* and *Schoenoxiphium* from *Carex* and *Uncinia*, and they further suggested that there was a special relationship between *Uncinia* and *Carex* subg. *Psyllophora* due to the groups' shared solitary spikes, unisexual spikelets, and completely fused utricles. Even though *Uncinia* can be delimited from *Carex* by female spikelets with hooked rachillae (i.e., hooked secondary axes; Figs. 1 and 3), early authors (Tuckerman, 1843; Drejer, 1844; Bentham, 1883; Clarke, 1883) questioned whether these genera were distinct due to the peculiar *C. microglochin* Wahlenb. (section *Leucoglochin* Dumort.), the only *Carex* to possess a consistently exsert rachilla like *Uncinia*. Once viewed as a circumscriptional problem, the discovery of another peculiar species, *U. kingii* Boott [= *C. kingii* (Boott) Reznicek], which has an exsert but only weakly hooked rachilla (Fig. 3), led to the conviction that the rachilla was a character of fundamental significance that demonstrated an indisputable phylogenetic link between *Carex* and *Uncinia* (Reznicek, 1990). This morphological transition series (Fig. 3), which focuses on either rachilla reduction or proliferation, is the source of nearly all controversy regarding *Uncinia* limits and classification, and it represents the most influential and disputed hypothesis used to construct the classic evolutionary scenarios proposed for the Cariceae (e.g., Kükenthal, 1909; Kreczetovicz, 1936; Nelmes, 1952; Savile & Calder, 1953; Hamlin, 1959). In conjunction with other evidence, such as phytogeography (Kükenthal, 1909; Nelmes, 1951, 1952) or smut host-parasite relationships (Savile & Calder, 1953), this hypothesis has been used to suggest an uncinoid origin for many *Carex* subg. *Psyllophora* species (Kreczetovich, 1936; Nelmes, 1952; Hamlin, 1959), as evidence that *Uncinia* had evolved from within *Carex* (Savile & Calder, 1953), that *Carex* itself was derived from *Uncinia* (Kükenthal, 1909), or simply that *Carex* and *Uncinia* should be merged (Koyama, 1961). However, recent studies of the inflorescence (Kukkonen, 1967; Meert & Goetghebeur, 1979) and rachilla (Reznicek, 1990) have suggested that *U. kingii* has more in common with *C. microglochin* than with *Uncinia* s. str. Accordingly, Reznicek (1990: 1419) transferred it to *Carex*, stating that the removal of *U. kingii* made "*Uncinia* a much more uniform and presumably natural genus."

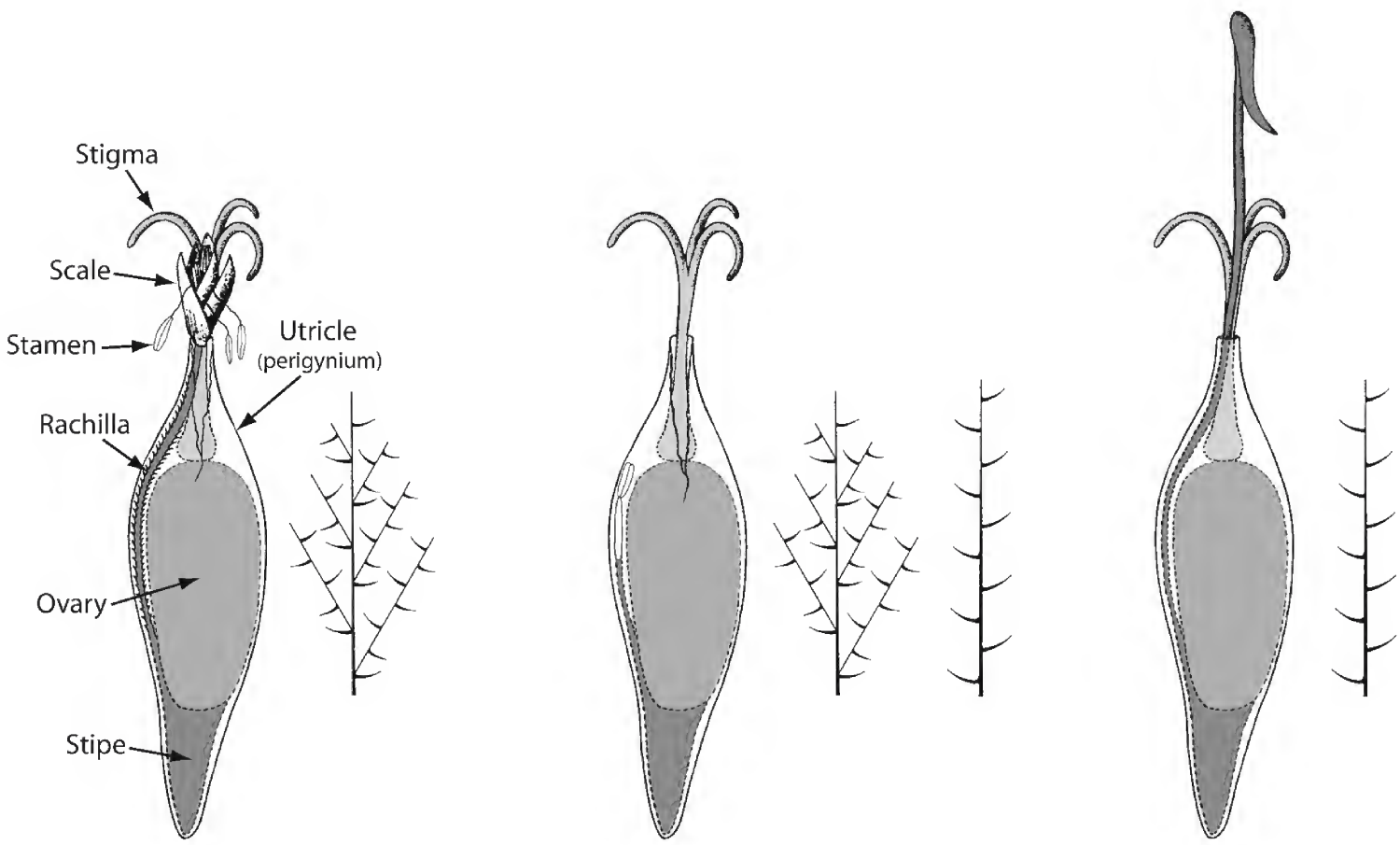

Figure 1. Cariceae generic circumscription. In his monograph of the tribe, Kükenthal (1909) divided genera largely on the basis of female spikelet morphology and the gross structure of the inflorescence. For each genus, typical spikelet morphologies are portrayed next to a stylized representation of their inflorescences (multispicate and/or unispicate). Note that the female spikelets in *Schoenoxiphium* and *Kobresia* have open utricles (i.e., not fused to apex) and rachillae that typically have male flowers at their apex, whereas *Uncinia* and *Carex* have closed utricles and sterile rachillae (i.e., when present). *Schoenoxiphium* can be distinguished from *Kobresia* by flattened rachillae with scabrous or ciliate margins that possess more highly developed male apices, whereas *Uncinia* is separated from *Carex* by hooked rachillae exsert from the utricle (see text and Fig. 3 for more details). *Cymophyllus,* which was segregated from *Carex* (Mackenzie, 1913), can only be separated from *Carex* subg. *Psyllophora* species by vegetative morphology. For a full description of generic features and variability, including problems with circumscription, see Starr et al. (2004). (Figure modified from Kükenthal, 1909; Kern, 1958; Mora Osejo, 1966.)

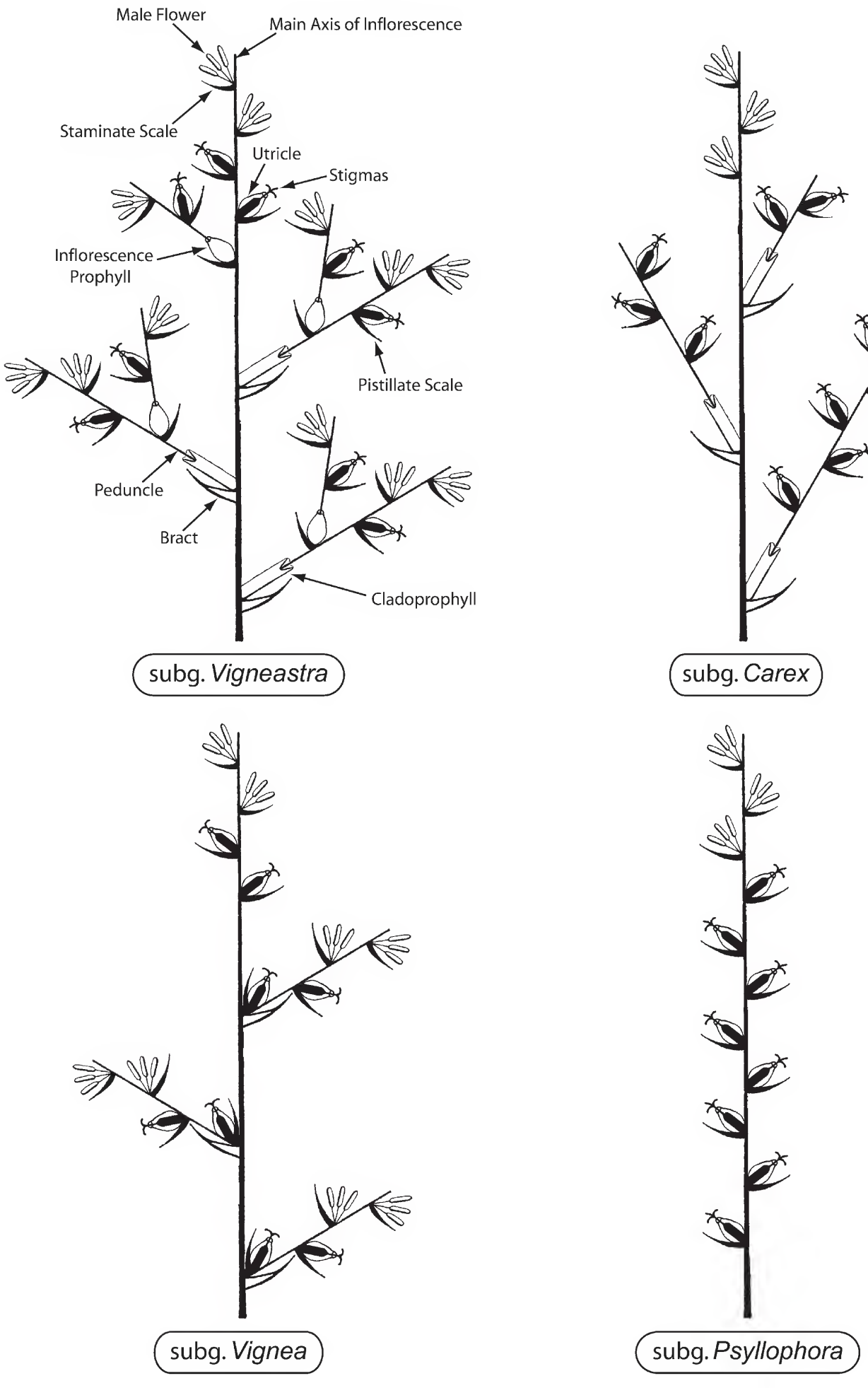

Figure 2. *Carex* subgeneric circumscription. Kükenthal (1909) divided *Carex* into four subgenera on the basis of gross inflorescence structure (unispicate vs. multispicate), the sexuality of spikes (unisexual vs. bisexual), and the presence/absence of peduncles and of tubular (cladoprophylls) or utricle-like prophylls (inflorescence prophylls sensu Reznicek, 1990). Using these characters and others that follow general trends, subgenus *Psyllophora* can be distinguished from other subgenera by a unispicate inflorescence; subgenus *Vignea* by sessile, bisexual spikes (androgynous and gynaecandrous), two stigmas (three exceptions), and the absence of cladoprophylls (four exceptions); subgenus *Vigneastra* by the presence of peduncled, bisexual spikes (androgynous) with cladoprophylls and inflorescence prophylls; and subgenus *Carex* by peduncled, predominately unisexual spikes (lateral females, terminal males) with cladoprophylls. For a full description of *Carex* subgeneric features and variability, including problems with circumscription, see Reznicek (1990) and Starr et al. (2004). (Figure modified from Kern, 1958.)

This is the second of two molecular analyses that focus on the relationships of the unispicate taxa of the Cariceae and their importance to resolving past infratribal classifications and evolutionary scenarios. Our previous study on the relationships of these taxa (Starr et al., 2004) suggested that there was a fundamental split within the unispicate species of the tribe. Dioecious species appeared to be related to multispicate taxa of either *Carex* subgenera *Carex* or *Vignea*, whereas the androgynous species of *Uncinia*, *Kobresia*, *Cymophyllus*, and *Carex* constituted a separate clade that included multispicate species of *Schoenoxiphium* and *Kobresia*. Topologies rejected the common links made between *Schoenoxiphium* and *Carex* subg. *Vigneastra* and the belief that *Schoenoxiphium* and *Kobresia* should be merged, while confirming the monophyly of subgenus *Vignea*, the polyphyly of subgenus *Psyllophora*, and the indistinct nature of subgenera *Carex* and *Vigneastra*. Moreover, this analysis supported the possibility of secondarily derived inflorescence units, and it suggested that cryptic morphological clades might be common in the Cariceae.

This present study concentrates on the outgroup relationships and former infrageneric classifications of *Uncinia*, with particular emphasis on the resolution of the classic transition series presented by the species of *Carex* subg. *Psyllophora* sect. *Leucoglochin* (*C. microglochin*, *C. parva* Nees, *C. pauciflora* Lightf.), *Uncinia kingii* [= *C. kingii*], and the genus *Uncinia* s. str. Despite the importance of these species to resolving the limits of *Uncinia* and numerous evolutionary scenarios, *C. microglochin*, *C. parva*, or *U. kingii* have not been included in previous molecular analyses of the tribe. The purpose of this study is to (1) examine generic and *Carex* subgeneric relationships within the tribe; (2) clarify the outgroup relationships of *Uncinia* for future phylogenetic studies; (3) resolve the historical controversy surrounding rachilla theories and the *Uncinia*/*Carex* sect. *Leucoglochin* transition series; and (4) evaluate former subgeneric and sectional classifications of *Uncinia* in the context of a molecular phylogeny.

Materials and Methods

Choice of Taxa and Outgroup

The taxonomy employed in this study and vouchers for all individuals used in molecular analyses are provided in Appendix 1. As in Starr et al. (2004), taxa were chosen to represent the range of morphological variation within the tribe and its major infratribal groups. Both "typical" exemplars of major historical groups and specific taxa that have played key roles in various evolutionary scenarios were employed in analyses. All 52 taxa included in the molecular phylogeny of the Cariceae by Starr et al. (2004) were used in the present analysis. Sampling included all five of the genera present in the analysis of Starr et al. (2004), and representatives from all four *Carex* subgenera (Kükenthal, 1909), although sampling was limited within the large subgenera *Vignea* (five species of ca. 450 spp.; Reznicek, 1990) and *Carex* (five species of ca. 1400 spp.; Reznicek, 1990). However, extensive sampling within these two subgenera was deemed unnecessary (Starr et al., 2004) because recent molecular studies have confirmed the monophyly of the "core" elements of both groups (Starr et al., 1999, 2004; Yen & Olmstead, 2000; Roalson et al., 2001). Taxonomic and geographic sampling for this prior molecular analysis was the most extensive to date for *Carex* subgenera *Vigneastra* (5/ca. 100 spp., representing Southeast Asia, Africa, and the Americas) and *Psyllophora* (13/ca. 70 spp., representing North America, Asia, Africa, South America, and New Zealand), and for the genera *Uncinia* (2/3 sections; 8/ca. 65 spp., representing South America, Australia, and New Zealand), *Kobresia* (3/4 sections; 7/ca. 50 spp., representing North America, Europe, and the Himalayas), and *Schoenoxiphium* (5/ca. 25 spp. representing the African mainland).

In order to examine the outgroup relationships and former infrageneric classifications of *Uncinia*, taxonomic sampling for this analysis was increased to include six additional species of *Carex* subg. *Psyllophora*, and seven additional species of *Uncinia*, including all previous ITS and ETS 1f sequences published for *Uncinia* (Starr et al., 2003, 2004). Sampling was focused on those members of subgenus *Psyllophora* traditionally linked to *Uncinia* (Kükenthal, 1909; Nelmes, 1952; Hamlin, 1959), especially the species of section *Leucoglochin* (*C. microglochin*, *C. parva*, *C. pauciflora*) and the cryptic *U. kingii*; these "transitional" taxa have provided the strongest historical evidence for evolutionary scenarios in the Cariceae. Owing to morphological variation in the bipolar *C. microglochin* (Kukkonen, 1970; Moore & Chater, 1971), both European and South American

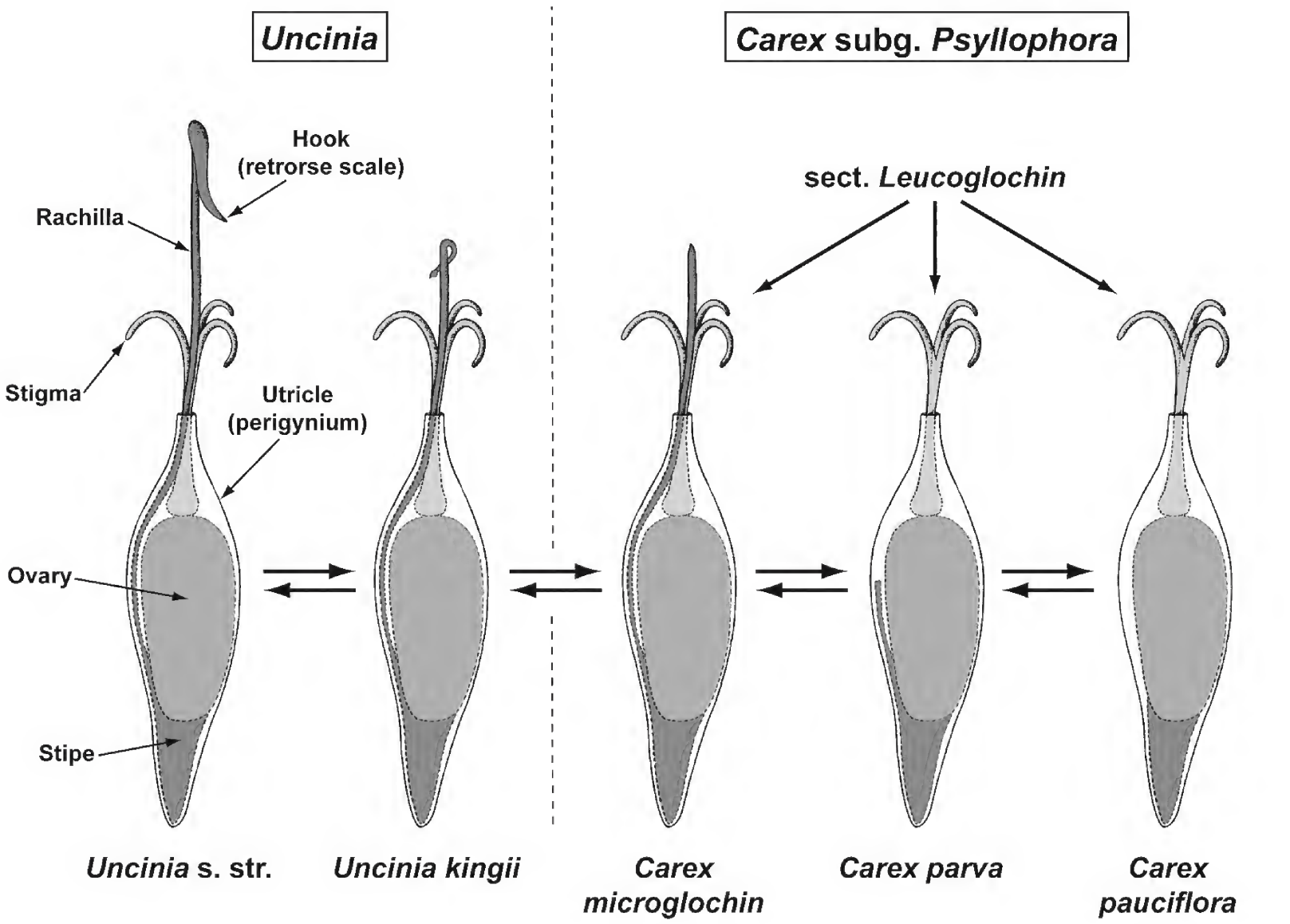

Figure 3. Female spikelets illustrating the historical transition series linking *Uncinia* to *Carex*. Elements of *Uncinia* or *Carex* are derived from each other via the growth or reduction of the rachilla and the gain or loss of hooks. Note that the hook in *U. kingii* is formed by the curvature of the rachilla, whereas in *Uncinia* s. str. it is formed by a retrorse inrolled scale. In *Carex*, the rachilla may be present or absent (e.g., *C. parva* vs. *C. pauciflora*), but it is never hooked. *Carex microglochin* is the only *Carex* where the rachilla is always exsert from the utricle (modified from Mora Osejo, 1966).

individuals were included. Collectively, sampling of subgenus *Psyllophora* in the present study represents approximately one third (i.e., 20 of 60 spp.) of the species recognized by Kükenthal (1909). In *Uncinia*, sampling increases mean that more than one third (24 spp.) of the genus is represented, including the historic representatives of the two subgenera and three sections proposed for the genus, and at least two taxa for each of the nine series described by Hamlin (1958, 1959). Only the monotypic series *Oceanicae* Hamlin (Hamlin, 1963) was not included.

MOLECULAR PROCEDURES, DNA ALIGNMENT, AND SEQUENCE ANALYSIS

DNA isolation, polymerase chain reaction (PCR) amplification, and sequencing of the ITS and ETS 1f regions were performed using the primers and procedures described in Starr et al. (1999, 2003). Leaves used for DNA extractions were only removed from pseudoculms with flowers. Betaine (Sigma # B-0300) was added to all PCR experiments to facilitate amplification (Starr et al., 2003) and to minimize amplicons from nonfunctional paralogues (Buckler et al., 1997). Exon (18S, 5.8S, and 26S nuclear ribosomal DNA [nrDNA]) and spacer (ITS 1, ITS 2, ETS 1f) boundaries were determined as for *Carex* (Starr et al., 1999) and *Uncinia* (Starr et al., 2003). To compare ITS sequences with those used by Starr et al. (2003, 2004) only ITS 1, ITS 2, and five bp at the 5′ end and 17 bp at the 3′ end of the 5.8S gene were used in analyses. ITS and ETS 1f sequences were initially aligned with CLUSTAL X (Thompson et al., 1997) then adjusted manually using parsimony (PAUP* 4.0b10; Swofford, 2002) as an objective cri-

Table 1. Sequence statistics for separate and combined ITS and ETS 1f data sets used in phylogenetic analyses. The 5.8S gene provided only four variable characters (three were parsimony-informative).

	ITS 1 + ITS 2	ETS 1f	nrDNA regions combined
Length range (bp)			
ingroup	425–449	584–600	1013–1045
outgroup included	425–512	528–600	1004–1045
Length mean (bp)			
ingroup	441.84	590.84	1032.7
outgroup included	443.20	589.19	1032.4
Aligned length (bp)			
ingroup	475	643	1118
outgroup included	535	644	1179
GC content range (%)			
ingroup	57.5–75.4	51.5–66.3	57.2–69.5
outgroup included	57.5–75.4	51.5–66.3	57.2–69.5
GC content mean (%)			
ingroup	69.9	59.8	64.1
outgroup included	69.8	58.7	64.0
Sequence divergence (%)			
ingroup	0.0–22.3	0.0–21.6	0.1–19.6
outgroup included	0.0–22.3	0.0–22.3	0.1–20.9
Sequence divergence mean (%)			
ingroup	10.8 ± 3.3	12.2 ± 4.1	11.6 ± 3.6
outgroup included	11.0 ± 3.4	12.6 ± 4.3	11.9 ± 3.7
No. of indels	55	61	116
Potentially informative indels	23	38	61
No. of variable sites	259 (53.1%)	393 (61.0%)	652 (57.6%)
Potentially informative sites	179 (36.7%)	288 (44.7%)	467 (41.3%)
Constant sites	229 (46.9%)	251 (39.0%)	480 (42.4%)
Uninformative sites	80 (16.4%)	105 (16.3%)	185 (16.3%)

terion for selecting among possible alignments (see Starr et al., 2004). The BASEFREQ and SHOWDIST commands in PAUP* were used to calculate uncorrected pairwise distances between individuals as well as sequence lengths and guanine-cytosine (GC) content. These statistics were used to evaluate sequence characteristics and to determine whether sequences might represent paralogues or external contamination.

PHYLOGENETIC ANALYSIS

Heuristic searches in PAUP* 4.0b10 (Swofford, 2002) of a combined ITS, ETS 1f, and insertion/deletion (indel) matrix were conducted using the MULTREES (save all minimal trees) and tree bisection-reconnection (TBR) commands for 5000 replicates of a RANDOM addition of taxa. ITS positions 71–100, 138–141, and 267–279 were excluded from all analyses due to the presence of repeated elements (71–100) or alignment ambiguity (138–141, 267–280). Indels were coded using the "simple" gap coding procedures of Simmons and Ochoterena (2000) as implemented in GapCoder (Young & Healy, 2003). After unusual patterns were discovered in sequence analyses involving *Carex filifolia* Nutt.,

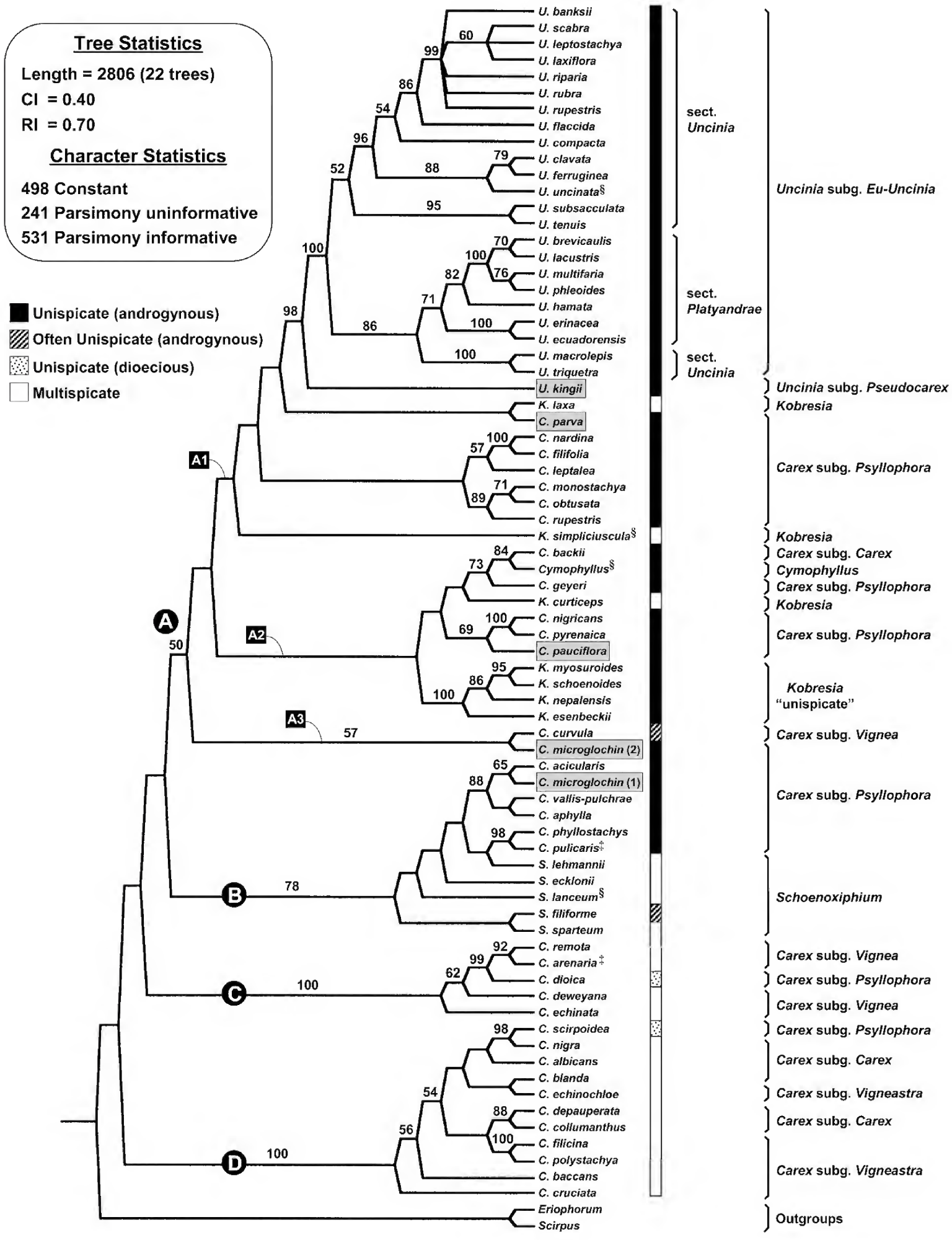

Figure 4. The strict consensus of the 22 most parsimonious trees discovered during heuristic searches. Tree and character statistics are given at the top left. Numbers above branches represent bootstrap values. Major clades described in the text are marked by circles (i.e., A, B, C, D), while minor clades are distinguished by squares (i.e., A1, A2, A3). The type species for Cariceae genera and *Carex* subgenera are marked respectively by (§) and (‡). *Uncinia kingii* and the members of *Carex* subg. *Psyllophora* sect. *Leucoglochin* are highlighted by gray rectangles. The bar to the right of specific epithets summarizes the gross inflorescence morphology of sampled species (the legend is to the left). Numbers in parentheses after epithets correspond to specific vouchers in Appendix 1. Except for *Cymophyllus,* generic names are abbreviated as follows: *S.* = *Schoenoxiphium, K.* = *Kobresia, U.* = *Uncinia, C.* = *Carex.* CI = consistency index; RI = retention index.

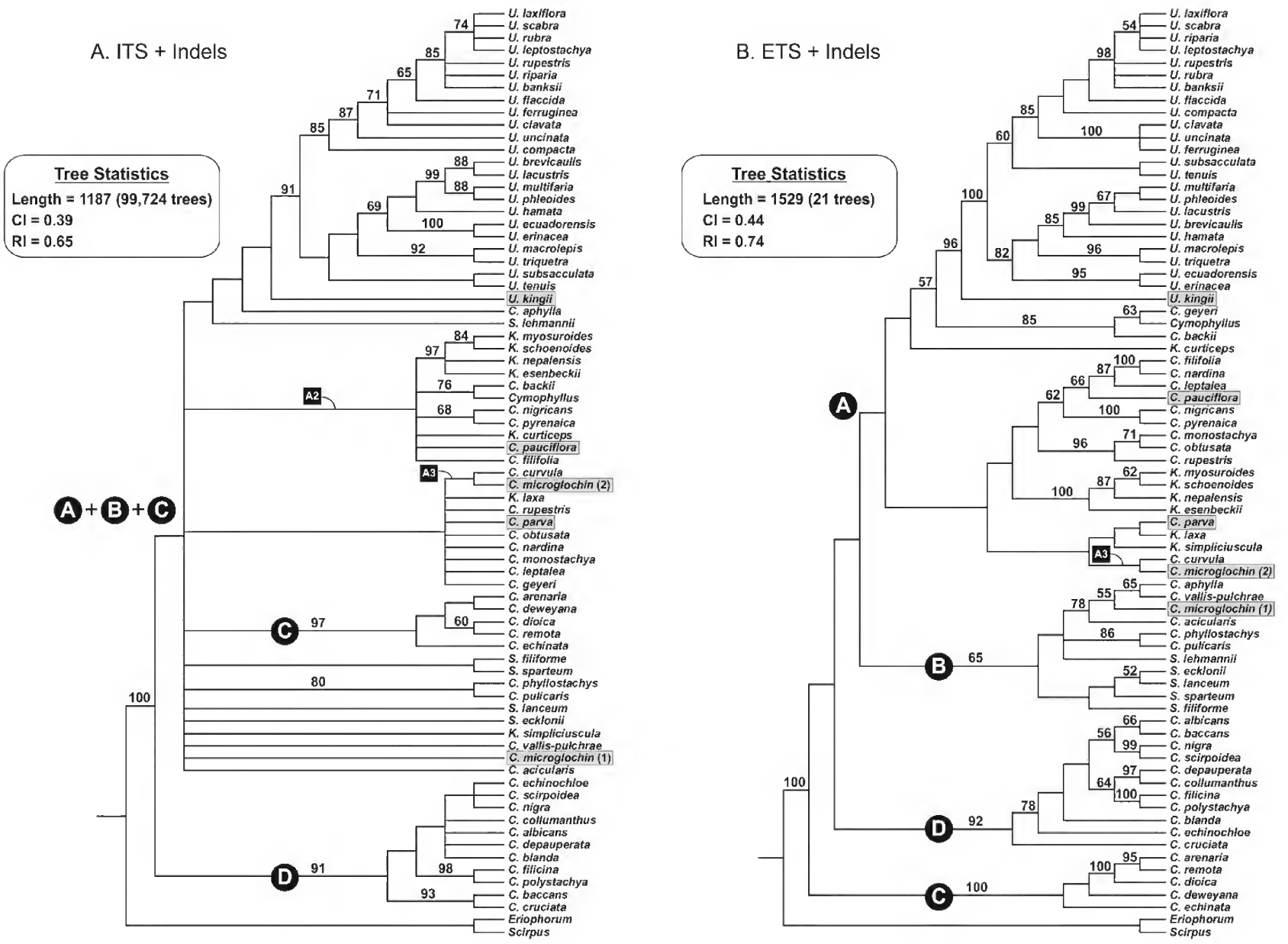

Figure 5. Strict consensus trees for separate ITS and ETS 1f parsimony analyses. —A. ITS plus indels analysis. —B. ETS 1f plus indels analysis. Tree statistics are given at the top left. Numbers above branches represent bootstrap values. Major clades described in the text are marked by circles (i.e., A, B, C, D), while minor clades are distinguished by squares (i.e., A2, A3). *Uncinia kingii* and the members of *Carex* subg. *Psyllophora* sect. *Leucoglochin* are highlighted by gray rectangles. Numbers in parentheses after epithets correspond to specific vouchers in Appendix 1. Except for *Cymophyllus,* generic names are abbreviated as follows: *S.* = *Schoenoxiphium, K.* = *Kobresia, U.* = *Uncinia, C.* = *Carex.*

a search excluding this taxon was also performed to determine whether it had an effect on tree topologies. *Carex filifolia* was included in all subsequent analyses. Separate heuristic searches of ITS and ETS 1f data sets were conducted with and without the inclusion of indels. These searches used TBR branch swapping and a RANDOM addition of taxa for 1000 replicates, with ITS analyses restricted to swapping on only 2000 trees per replicate (NCHUCK = 2000) for time reasons. Clade support was assessed via the bootstrap (BS; Felsenstein, 1985). For all analyses, BS values were derived from 10,000 replicates using a heuristic search strategy, TBR branch swapping, and a SIMPLE stepwise addition of taxa with the MULTREES option "off." DeBry and Olmstead (2000) have shown that this type of search strategy rapidly produces bootstrap proportions that are essentially identical to the values produced by TBR searches with the MULTREES option "on." As in Starr et al. (2004), BS support was categorized as very poor or very weak (< 55%), poor or weak (55%–64%), moderate (65%–74%), good or well (75%–84%), very good or very well (85%–94%), or strong (95%–100%) based on the simulation studies of Hillis and Bull (1993) and Huelsenbeck et al. (1996). Homoplasy levels and character support for trees were assessed by the consistency index (CI; Kluge & Farris, 1969) and retention index (RI; Farris, 1989).

An incongruence length difference (ILD) test (Farris et al., 1994) of the combined ITS and ETS 1f

Figure 6. Maximum likelihood tree resulting from heuristic searches of the combined Cariceae ITS and ETS 1f data assuming a GTR + G + I model of sequence evolution. Branches whose confidence intervals do not exclude zero at the $P = 0.05$ level are marked by asterisks. Major clades described in the text are marked by circles (i.e., A, B, C, D), while minor clades are distinguished by squares (i.e., A3). The type species for Cariceae genera and *Carex* subgenera are marked respectively by (§) and (‡). *Uncinia kingii* and the members of *Carex* subg. *Psyllophora* sect. *Leucoglochin* are highlighted by gray rectangles. Except for *Cymophyllus,* generic names are abbreviated as follows: *S. = Schoenoxiphium, K. = Kobresia, U. = Uncinia, C. = Carex.*

data sets (indels included) was also performed in PAUP* using a heuristic search strategy, TBR branch swapping, and a RANDOM addition of taxa (25 replicates per partition, NCHUCK = 100) for 264 random partitions of the data (constant characters were excluded, $\alpha = 0.01$; Cunningham, 1997; Darlu & Lecointre, 2002). Although this test is considered to be the best parsimony-based method for evaluating data set congruence (Cunningham, 1997), the interpretation of the test and its validity have been questioned (e.g., Yoder et al., 2001; Dowton & Austin, 2002). In this study, the test was performed simply to acknowledge the possibility of incongruence between the data sets, even though a "total evidence" approach was taken (Kluge, 1989; Nixon & Carpenter, 1996).

Maximum likelihood (ML) trees were estimated by heuristic searches (TBR, RANDOM addition of taxa, 10 replicates) of the combined ITS/ETS 1f data set (indels excluded) using a general time-reversible (GTR) model that incorporated a correction for rate heterogeneity across sites (i.e., a gamma distribution, G; Yang, 1993) and an estimate of the proportion of invariable characters (I). The GTR + G + I model was chosen by Modeltest 3.06 (Posada & Crandall, 1998), a program that uses likelihood ratio tests and the Akaike information criterion to identify which of 56 nested evolutionary models is optimal for the data. The ZEROLENTEST command in PAUP* ("full" optimization) was used to determine whether branch lengths in the best ML tree were significantly greater than zero.

Owing to low branch support, Shimodaira and Hasegawa (SH; 1999) tests comparing the optimal ML tree with trees where section *Leucoglochin* (with and without *Uncinia kingii*) and a section *Leucoglochin* + *Uncinia* s. str. clade were forced to be monophyletic were used to test the common hypotheses that section *Leucoglochin* is natural and a direct relative of the genus *Uncinia*. The same analyses were performed with constraint trees that included only those individuals of section *Leucoglochin* common to Clade A after unusually high levels of sequence divergence were detected in *Carex microglochin* (see below). One million bootstrap replicates using the re-sampling estimated log-likelihood method (RELL) of Kishino et al. (1990) were used to generate the SH test distribution in PAUP*.

RESULTS

SEQUENCE ANALYSIS

Summary statistics for the 75 taxa used in the combined ITS and ETS 1f Cariceae analysis are given in Table 1. The 5.8S gene was 166 bp long in all taxa sequenced due to a 3 bp insertion that is common to most Cyperaceae.

Pairwise sequence divergence within Cariceae for the combined ITS and ETS 1f data set ranged from 0.0% to 19.6% (*Uncinia triquetra* Kük. × *Carex baccans* Nees). On average, ETS 1f was more variable than ITS, with most pairwise comparisons (75.8%) showing a higher divergence for ETS 1f than for ITS (Table 1). Notable exceptions to this rule were seen in most pairwise comparisons involving *C. filifolia*. This taxon possessed the lowest GC content (58.4%), the second shortest *Carex* sequence (421 bp), the highest average ITS divergence with other Cariceae (18.9% ± 2.3%), and the largest average disparity between pairwise ITS versus ETS 1f divergence (+5.6% ± 3.3%). The disparity between ITS and ETS 1f divergence in comparisons of *C. filifolia* versus *C. nardina* Fr. (ITS = 22.3%, ETS 1f = 0.2%) was particularly noteworthy.

Infraspecific divergence between the two *Carex microglochin* individuals sequenced in this study was high for both the ITS (10.7%) and ETS 1f (9.7%) regions. In the combined data set, Scottish *C. microglochin* was most similar to *C. rupestris* All. (7.2% divergence), whereas Ecuadorian *C. microglochin* was least divergent (4.4% to 5.3%) with three South American carices (*C. acicularis* Boott, *C. aphylla* Kunth, and *C. vallis-pulchrae* Phil.). Ecuadorian *C. microglochin* shared a unique 5.8S mutation (C→T) with *C. acicularis*, *C. aphylla*, and *C. vallis-pulchrae* in a highly conserved portion of the gene (position 130; data not shown). GC contents (ITS, 71.9%–72.9%; ETS 1f, 57.0%–61%) and spacer lengths (ITS, 441–443 bp; ETS 1f, 589–592 bp) for both *C. microglochin* sequences were close to the mean values for ingroup taxa (Table 1). The aligned matrix used for all phylogenetic analyses is available online from TreeBASE (www.treebase.org/treebase/).

PHYLOGENETIC ANALYSES

Aligned sequences for the combined ITS and ETS 1f data set, including small portions of the 5′

and 3′ ends of the 5.8S gene in all Cariceae taxa, resulted in a matrix of 1317 characters (116 indels), of which 47 were excluded from analyses due to repeats or alignment ambiguity. Of the remaining 1270 characters, 498 (39.2%) were constant, 241 (19.0%) were parsimony-uninformative, and 531 (41.8%) were parsimony-informative. No topological differences were detected between parsimony analyses that included and excluded *Carex filifolia*. ILD tests suggested that ITS and ETS 1f data sets were incongruent ($P = < 0.01$).

Heuristic searches under the parsimony criterion for the combined ITS and ETS 1f data set discovered 22 trees, 2806 steps each. The strict consensus of these 22 most parsimonious trees (MPTs) is given in Figure 4. This tree suggests that the tribe consists of four primary clades: (1) a very weakly supported clade (Clade A, 50% BS) composed of species of *Uncinia*, *Kobresia*, *Cymophyllus*, unusual members of *Carex* subgenera *Vignea* (*C. curvula* All.) and *Carex* (*C. backii* Boott), and a majority of the androgynous species of *Carex* subg. *Psyllophora* p.p.; (2) a clade with good support (Clade B, 78% BS), sister to Clade A, that consists of *Schoenoxiphium* species and a smaller group of androgynous species of *Carex* subg. *Psyllophora* p.p.; (3) a strongly supported clade (Clade C, 100% BS), sister to Clades A and B, that consists of "typical" multispicate members of *Carex* subg. *Vignea*, and a single, dioecious species of *Carex* subg. *Psyllophora* (*C. dioica* L.); and lastly, (4) a strongly supported clade (Clade D, 100% BS) comprising "typical" multispicate members of *Carex* subgenera *Carex* and *Vigneastra*, and a single dioecious species of *Carex* subg. *Psyllophora* (*C. scirpoidea* Michx.).

Within Clade A, two very poorly supported clades (A1, A2) and one poorly supported clade (A3) are evident. These three clades each possess one of the three members of section *Leucoglochin* (Fig. 4). The first clade (A1, < 50% BS; Fig. 4), consisting of the genus *Uncinia*, *Carex* subg. *Psyllophora* p.p., and two multispicate members of the genus *Kobresia*, provides strong support for the monophyly of *Uncinia* s.l. (98% BS) and for a sister group relationship between *U. kingii* (i.e., subgenus *Hemihamatae* (Hamlin) Kukkonen) and *Uncinia* s. str. (i.e., subgenus *Eu-Uncinia* Kük. sections *Uncinia* and *Platyandrae* C. B. Clarke). Within *Uncinia* s. str., two major groups are found: (1) a very weak (52% BS) clade of section *Uncinia* species, and (2) a very well-supported (86% BS) clade consisting of a monophyletic section *Platyandrae* (71% BS) sister to section *Uncinia* series *Macrolepidae* Hamlin (100% BS). With the exception of series *Australes* Hamlin (section *Uncinia* clade) and series *Macrolepidae*, *Macrotrichae* Hamlin, and *Trichocarpae* Hamlin (section *Platyandrae*/series *Macrolepidae* clade), trees suggest the series circumscriptions in *Uncinia* are either paraphyletic or polyphyletic. Topologies within Clade A1 also place a very weakly supported clade (< 50% BS) containing the multispicate *K. laxa* Nees and the unispicate *C. parva* (section *Leucoglochin*) as sister to *Uncinia* s.l., while another very weakly supported clade provides very good support for a group comprising elements of *Carex* sections *Obtusatae* (Tuck.) Mack. (*C. obtusata* Lilj.), *Rupestres* (Tuck.) Meinsh. (*C. rupestris*), and *Longespicatae* Kük. (*C. monostachya* A. Rich.), and strong support for a *C. filifolia* + *C. nardina* clade (sections *Filifoliae* (Tuck.) Mack. and *Nardinae* (Tuck.) Mack.). *Kobresia simpliciuscula* (Wahlenb.) Mack., the type of the genus, is found at the base of Clade A1.

The second clade (Clade A2; Fig. 4), consisting of *Kobresia*, the monotypic genus *Cymophyllus*, and several members of *Carex* subg. *Psyllophora*, provides strong support (100% BS) for the monophyly of the unispicate species of *Kobresia* and good support (84% BS) for a sister group relationship between the genus *Cymophyllus* and a unispicate member of *Carex* subg. *Carex* sect. *Phyllostachyae* Tuck. ex Kük. (*C. backii*). Moderate support (69% BS) is also seen for a clade comprising a monophyletic *Carex* sect. *Dornera* Heuff. (*C. nigricans* C. A. Mey. and *C. pyrenaica* Wahlenb.; 100% BS) sister to *C. pauciflora* (section *Leucoglochin*).

The third and last group (Clade A3) is a weak clade (57% BS) consisting of the unusual *Carex curvula* (*Carex* subg. *Vignea* sensu Kükenthal) and European *C. microglochin* (section *Leucoglochin*; Fig. 4).

Relationships within Clade B place a paraphyletic *Schoenoxiphium* at the base of a clade containing mostly androgynous *Carex* subg. *Psyllophora* species (Fig. 4). Only two groups are noteworthy, a clade with very good support (88% BS) consisting of South American members of subgenus *Psyllophora* (sections *Aciculares* (Kük.) G. A. Wheeler, *Leucoglochin*, and *Junciformes* (Boeck.) Kük.) including Ecua-

dorian *C. microglochin*, and a strongly supported clade (98% BS) comprising *C. pulicaris* L. (section *Psyllophora* (Degl.) Koch) and *C. phyllostachys* C. A. Mey. (section *Caryotheca* V. I. Krecz. ex T. V. Egorova).

Clade C is a strongly supported group (100% BS) of predominately multispicate European and North American species of *Carex* subg. *Vignea* (Fig. 4). The nested position of *C. dioica*, a dioecious species of *Carex* subg. *Psyllophora*, is the most noteworthy relationship of the group.

The last group, Clade D, is a strongly supported clade (100% BS) that suggests *Carex* subgenera *Carex* and *Vigneastra* are unnatural, and that *C. scirpoidea*, a dioecious member of *Carex* subg. *Psyllophora*, is a close relative of *Carex* subg. *Carex* species (Fig. 4).

Separate analyses of ITS and ETS 1f data (indels included) respectively produced 99,724 MPTs, 1187 steps long, and 21 MPTs, 1529 steps long. The strict consensus trees for both analyses are given in Figure 5. Notable topological differences between these two trees include the more highly resolved and statistically supported ETS 1f versus ITS analysis, and the positioning of Clade D (ITS analysis) as opposed to Clade C (ETS 1f analysis) as sister to all other Cariceae. Clades A and B were only resolved as monophyletic in ETS 1f analyses, although an A + B clade was seen in ITS analyses that excluded indels (results not shown). All separate ITS and ETS 1f analyses positioned *Uncinia kingii* as sister to *Uncinia* s. str., although ITS support for this relationship was very poor. Clades with good support in either the ITS or ETS 1f analysis were also present in the strict tree for combined analyses. Clade A1 was not resolved in separate analyses.

GTR + G + I model settings used in all ML searches and SH tests are as follows: base frequencies (A = 0.1392, C = 0.3062, G = 0.3399, T = 0.2147), rate matrix ([A–C] = 0.7276, [A–G] = 3.5474, [A–T] = 1.1872, [C–G] = 0.5293, [C–T] = 5.3786, [G–T] = 1.0000), gamma (G) shape parameter = 0.7737, proportion of invariable sites (I) = 0.1498. ML searches of the combined data set produced a single tree with a –ln likelihood (–ln *L*) of 14439.87248 (Fig. 6). This tree recovers the same four major clades (i.e., A, B, C, D) as parsimony analyses, with differences between analyses confined to rearrangements around weak nodes that do not affect general conclusions. Potentially important topological differences in the ML tree, such as a monophyletic *Schoenoxiphium* and a C + D clade, occur at branches that are not significantly different from zero (Fig. 6). SH tests indicate that ML and parsimony trees are not statistically different (Table 2).

SH tests of ML trees that forced section *Leucoglochin* (with and without *Uncinia kingii*) and a section *Leucoglochin* + *U. kingii* + *Uncinia* s. str. clade to be monophyletic were all significantly different from the optimal ML tree when Ecuadorian *Carex microglochin* was included in constrained clades (Table 2). When Ecuadorian *C. microglochin* was excluded from constrained clades, only analyses that forced a section *Leucoglochin* + *U. kingii* clade were found to be significantly different from the optimal ML tree.

Discussion

Sequence Analysis

The size, sequence divergence, and GC contents for the taxa sequenced in this study are comparable to the values seen in previous Cariceae studies that have used the ITS (Roalson et al., 2001; Starr et al., 1999, 2003, 2004) and ETS 1f (Starr et al., 2003, 2004) regions. It is now clear that the three base pair insertion at the 5′ end of the 5.8S gene first discovered by Starr et al. (1999) is a feature common to all Cariceae, but not to all Cyperaceae genera (Roalson & Friar, 2000; Roalson et al., 2001; Starr et al., 2007). Starr et al. (2007) have shown that this insertion is not only useful for delimiting the Cyperaceae, but its pattern of loss and even point mutations within its sequence are useful for defining clades at multiple taxonomic levels. On average, the ETS 1f region is more variable than ITS, which is consistent with the results of most previous angiosperm studies (e.g., Baldwin & Markos, 1998; Bena et al., 1998a, b; Vander Stappen et al., 2003). However, studies within the Cyperaceae have also shown that the ETS 1f region may be as variable or even more conserved than ITS depending on the group studied (Starr et al., 2003; Ford et al., 2006).

In plants, the nrDNA region consists of hundreds to thousands of copies that are tandemly repeated at one or more loci (Baldwin et al., 1995). Variation among these repeats is typically low within species as a consequence of the homogenizing

effects of concerted evolution. This fact is often used to justify minimal sampling within species (typically one individual) since amplicons should be orthologous if speciation is divergent, recombination is absent, and repeat homogenization is complete and maintained over time (Baldwin et al., 1995; Álvarez & Wendel, 2003). Since these assumptions are often violated, the genome of any individual sampled for the nrDNA region may contain paralogues that could confound phylogenetic inference (Hershkovitz et al., 1999; Álvarez & Wendel, 2003). One of the most common sources of nrDNA paralogues within individuals comes from pseudogenes, non-expressed repeats whose relaxed functional constraints are typically revealed by high rates of evolution (Hershkovitz et al., 1999; Álvarez & Wendel, 2003). These nrDNA pseudogenes can sometimes be identified by their large indels, low GC contents, and high sequence divergence, among other features (Buckler & Holtsford, 1996a, b; Buckler et al., 1997). In considering these characteristics, the ITS region of *Carex filifolia* in particular stands out. The consistently high divergence of *C. filifolia* ITS with other taxa, its low GC content, and short length suggest that this sequence may not be under the same selective pressures as a functional ITS region. Moreover, this sequence was not amplified using dimethyl sulfoxide (DMSO) or betaine (Starr et al., 1999). These DNA denaturing or destabilizing cosolvents may be essential PCR additives if functional ITS sequences with high GC contents are to be preferentially amplified over presumably nonfunctional paralogues with low GC contents (Buckler & Holtsford, 1996a; Buckler et al., 1997; Starr et al., 2003; Ford et al., 2006). Further specimens of *C. filifolia* will need to be amplified, cloned, and sequenced to confirm whether the ITS region used in this analysis is a paralogue. The surprisingly low ETS 1f divergence of *C. nardina* × *C. filifolia* does not appear to be the result of contamination as their DNAs were extracted, amplified, and sequenced at least four months apart.

Previous studies that have looked at Cariceae infraspecific variation within the ITS (Starr et al., 1999, 2003; Ford et al., 2006) and ETS 1f (Starr et al., 2003; Ford et al., 2006) regions have generally found levels of sequence divergence to be low (< 1.0%). It is for this reason that the level of divergence detected between Ecuadorian and Scottish samples of *Carex microglochin* is surprising. It is possible that the presence of ITS or ETS 1f paralogues, maybe as a consequence of hybridization, pseudogenes, or other factors (see section "Taxonomy of *Carex microglochin*" below), may account in part for the incongruence detected by the ILD test in this and other Cariceae studies (Roalson et al., 2001; Starr et al., 2004; Ford et al., 2006).

GENERAL RELATIONSHIPS WITHIN THE CARICEAE

Apart from minor branch re-arrangements within Clade A and slight differences in the relationships of *Schoenoxiphium* species at the base of Clade B, the present analysis is entirely consistent with the previous tribal analysis of Starr et al. (2004). Phylogenetic analyses indicate that *Uncinia* is monophyletic and part of a large clade (Clade A) consisting of *Kobresia*, *Cymophyllus*, the unusual *Carex curvula* (subgenus *Vignea*), and unispicate members of *Carex* subgenera *Carex* (section *Phyllostachyae*) and *Psyllophora*. This clade is sister to a clade (Clade B) composed of the genus *Schoenoxiphium* and various members of *Carex* subg. *Psyllophora*. The remaining species fall into two groups, one consisting of "typical" members of *Carex* subg. *Vignea* and a dioecious member of *Carex* subg. *Psyllophora* (*C. dioica*), and the second comprising "typical" members of *Carex* subgenera *Carex* and *Vigneastra*, and a dioecious member of *Carex* subg. *Psyllophora* (*C. scirpoidea*).

Such topologies strongly indicate that the genus *Carex* as presently circumscribed is artificial. Moreover, analyses support proposals to merge *Carex* subgenera *Vigneastra* and *Carex* (e.g., Ohwi, 1936; Koyama, 1962), and they confirm the general consensus that *Carex* subg. *Vignea* is natural (e.g., Nelmes, 1951; Koyama, 1962; Reznicek, 1990), and that subgenus *Psyllophora* is polyphyletic (e.g., Kreczetovicz, 1936; Nelmes, 1952; Smith & Faulkner, 1976). Analyses also reject many long-held hypotheses of homology that would support a monophyletic *Schoenoxiphium* and *Kobresia* (e.g., Nelmes, 1951; Kern, 1974; Smith & Faulkner, 1976), or a phylogenetic link between *Carex* subg. *Vigneastra* and *Schoenoxiphium* (e.g., Kükenthal, 1909; Smith & Faulkner, 1976; Reznicek, 1990). Of direct relevance to this study, analyses continue to support a fundamental split among unispicate

Table 2. Shimodaira-Hasegawa (SH) tests comparing optimal maximum likelihood (1, GTR + G + I) and parsimony (2–3) trees, with trees where section *Leucoglochin*, *Uncinia kingii,* and *Uncinia* s. str. were successively forced to be monophyletic (4, *Leucoglochin* only; 5, *Leucoglochin* + *Uncinia kingii*; 6, *Leucoglochin* + *Uncinia kingii* + *Uncinia* s. str.; trees 7–9 represent the same analyses minus Ecuadorian *Carex microglochin*). Tests are one-tailed and were conducted assuming a GTR + G + I model of sequence evolution. Indel characters were not included in the calculation of tree length. Asterisks (*) next to *P* values indicate significance at the $\alpha = 0.05$ level.

Tree	−ln *L*	−ln *L* Difference	Steps	SH-test *P* value
1 (Optimal ML Tree)	14439.87248	(best)	2638	—
2 (Parsimony–best)	14477.58380	37.71133	2612	0.26
3 (Parsimony–worst)	14483.54808	43.67561	2612	0.22
4 (*Leucoglochin*)	14565.07607	125.20359	2694	< 0.001*
5 (*Leucoglochin* + *U. kingii*)	14610.22162	170.34914	2713	< 0.00001*
6 (*Leucoglochin* + *U. kingii* + *Uncinia*)	14569.85179	129.97932	2686	< 0.0001*
7 (*Leucoglochin*–*C. microglochin* 1)	14475.04083	35.16836	2662	0.29
8 (*Leucoglochin* + *U. kingii*–*C. microglochin* 1)	14521.44463	81.57216	2682	0.02*
9 (*Leucoglochin* + *U. kingii* + *Uncinia*–*C. microglochin* 1)	14485.04641	45.17394	2659	0.16

species where the dioecious members of *Carex* subg. *Psyllophora* are related to multispicate species in either *Carex* subgenera *Carex* or *Vignea*, while the androgynous unispicate members of *Carex* subgenera *Carex* and *Psyllophora*, and the genera *Cymophyllus*, *Kobresia*, and *Uncinia*, are variously placed in a clade that also contains multispicate species of *Schoenoxiphium* and *Kobresia* (Starr et al., 2004). In addition, the firm position of the monotypic genus *Cymophyllus* within Clade A is morphologically consistent with the taxonomic composition of these clades. This supports treatments that regard *Cymophyllus* as a common ally of *Carex* subg. *Psyllophora* species (Kükenthal, 1909).

Despite considerable sampling differences among molecular analyses of the tribe (Yen & Olmstead, 2000; Roalson et al., 2001; Starr et al., 2004), a general consensus among studies appears to be emerging. Even though the arrangement of clades differs from one analysis to the next, three of the four major clades (i.e., Clades A, C, D) described in this analysis are consistent with clades discovered in the chloroplast analysis of Yen and Olmstead (2000) and the combined ITS and *trnT-L-F* analysis of Roalson et al. (2001). Clade B, on the other hand, is novel to this analysis and the analysis of Starr et al. (2004). However, previous analyses have not sampled androgynous *Carex* subg. *Psyllophora* from South America or Europe, or the diversity of taxa sampled within *Schoenoxiphium* for these analyses. Nonetheless, it is interesting to note that the only species of *Schoenoxiphium* sampled in the analysis of Roalson et al. (2001) was sister to taxa representing Clade A.

Regardless of topological congruence among molecular analyses, poor statistical support both within and between the major groups of the Cariceae clearly indicates that assigning clades to the basal node of the tribe is still premature. Moreover, it would be unwise to imply that the conclusions drawn from the present phylogeny will not be affected by future increases in characters or taxa. Nevertheless, the consistency of molecular analyses does represent a considerable step forward for rejecting many historical hypotheses that have defied resolution, and for suggesting future systematic problems that need to be clarified.

OUTGROUPS, RACHILLA THEORIES, AND THE RELATIONSHIPS OF *UNCINIA* AND *CAREX* SECT. *LEUCOGLOCHIN*

The relationships of the unispicate species of *Uncinia* and *Carex* subg. *Psyllophora* have constitut-

ed one of the most difficult and perplexing problems in Cariceae systematics (Reznicek, 1990). The extreme reduction of these two groups has obscured their relationships to the point where even intense studies of tribal inflorescence development have only been able to conclude that they may represent reduced forms of practically any branched inflorescence in the tribe (Smith & Faulkner, 1976; Timonen, 1998). However, the well-developed rachilla of *C. microglochin*, a trait ascribed to other Cariceae genera, combined with the apparently intermediate *U. kingii*, appeared to demonstrate that *Uncinia*, *Carex*, or *Carex* p.p. had evolved from each other via the reduction or proliferation of the rachilla (Kükenthal, 1909; Kreczetovich, 1936; Nelmes, 1952; Savile & Calder, 1953; Hamlin, 1959). Although the evolutionary direction and the specific derivatives of this historic transition series have often been debated, the validity of the transition series itself has only been questioned by Kern (1958) and Reznicek (1990). While Kern (1958) attacked the transition series from a philosophical point of view, Reznicek (1990) recognized that there was compelling evidence from both the study of the inflorescence (Kukkonen, 1967; Meert & Goetghebeur, 1979) and rachilla to suggest that *U. kingii* was more closely related to *C. microglochin* and its allies than it was to *Uncinia* s. str. *Uncinia kingii* had "… nothing in common with *Uncinia* except the superficially similar but independently evolved hook" (Reznicek, 1990: 1419). Moreover, it was "… not a species of remarkable phylogenetic interest … simply a *Carex* very closely related to *C. microglochin* and its allies …" (Reznicek, 1990: 1419).

The present analysis appears to agree with Reznicek (1990) that *Carex* s. str., comprising the multispicate subgenera of the genus, is only distantly related to *Uncinia*, but unlike Reznicek (1990), it also suggests that androgynous species of *Carex* subg. *Psyllophora* are more closely related to *Uncinia*, *Kobresia*, *Schoenoxiphium*, and *Cymophyllus* than they are to *Carex* s. str. Furthermore, this study solidly supports a monophyletic *Uncinia* that includes *U. kingii* [= *C. kingii*], and topologies suggest that section *Leucoglochin* (minus *U. kingii*) is neither natural nor monophyletic with *Uncinia* (but see below; Table 2). These are surprising results since Reznicek's (1990) argument that *U. kingii* was more closely related to *C. microglochin* and its allies than it was to *Uncinia* s. str. is compelling (e.g., Wheeler, 1993–1994), and historically section *Leucoglochin* has commonly been considered as an homogeneous group (e.g., Nelmes, 1952; Reznicek, 1990). Moreover, there appears to be no conspicuous morphological apomorphy that can distinguish *Uncinia* s. str. and *U. kingii* from their sister groups since the hook in *U. kingii* (formed via a curvature of the rachilla axis; Kukkonen, 1967) is not homologous to the hook of *Uncinia* s. str. (formed via a retrorse inrolled scale; Kukkonen, 1967). Such evidence would seem to contradict the validity of the present results; however, the clade within which *Uncinia* is found is highly consistent with previous molecular analyses (see above). Therefore, given the historical inability of authors to determine confidently the relationships of *Carex* subg. *Psyllophora* and *Uncinia* due to their highly reduced inflorescences (e.g., Smith & Faulkner, 1976; Reznicek, 1990), the relationship between *Uncinia* s. str. and *U. kingii* is here interpreted as further evidence that cryptic clades may be common in the Cariceae (Starr et al., 2004). Nonetheless, more data from multiple independent markers are needed to strengthen the current hypothesis and to better assess whether topologies in this and in previous analyses could have been affected by systematic (e.g., natural hybridization, long-branch attraction) and/or random error (sampling artifacts). The very weak support for many groups in Clades A and B, the significant ILD test, and the inability of the data to entirely reject a monophyletic section *Leucoglochin* or section *Leucoglochin* + *Uncinia* clade (i.e., minus Scottish *C. microglochin*) suggest that phylogenetic analyses may have been influenced by some type of error.

If cryptic clades are common in the Cariceae, does this mean that most clades may be impossible to distinguish by morphological synapomorphies? Not necessarily: morphological synapomorphies may be few and groups largely polythetic, but a re-examination of features within the context of phylogeny is likely to reveal new, possibly obscure, homologues. For example, in the case of *Uncinia kingii* and *Uncinia* s. str., the primary morphological structures that form the hook may be analogous, but the bend in the rachilla at the point where the hook begins (cf. figs. 18, 20, and 21 in Reznicek, 1990, and figs. 5 and 6 in Kukkonen, 1967) could be homologous. If the hook formed after this bend pro-

vided *U. kingii* and *Uncinia* s. str. with a key selective advantage such as epizoochorous dispersal (Hamlin, 1959; Mora Osejo, 1966; Starr, pers. obs.), then the considerably more efficient scale versus rachilla mechanism in *Uncinia* s. str. could explain why it is so much more diverse than its sister group. Further anatomical and micromorphological studies of the cells in the bend region of the rachilla may be able to test this hypothesis of homology.

In the history of Cariceae classifications and evolutionary theories, the rachilla has played a central role in indicating the evolutionary position, time, means, and origin of *Carex* subg. *Psyllophora*. Although this analysis rejects Reznicek's (1990) ideas and places *Uncinia kingii*, *Carex* sect. *Leucoglochin* p.p., and many androgynous members of subgenus *Psyllophora* within a single clade, this does not mean that the remaining "rachilla" theories are now credible. It is abundantly clear that the genera in the Cariceae cannot be arranged in a simple evolutionary series as envisioned by Kükenthal (*Schoenoxiphium*→*Kobresia*→*Uncinia*→*Carex* subg. *Psyllophora*→*Carex* s. str.; 1909), and that this analysis does not support the origin of *Carex* subg. *Psyllophora* from within *Uncinia*. Furthermore, despite the fact that this analysis agrees with Kreczetovicz (1936) that subgenus *Psyllophora* is polyphyletic, and that sections *Dioicae* (Tuck.) Pax and *Scirpinae* (Tuck.) Kük. may have their origins from within *Carex* subgenera *Vignea* and *Carex*, the analysis excludes a common origin for *Uncinia* and the androgynous subgenus *Psyllophora* from *Carex* subg. *Vigneastra*, and it rejects the notion that *C. microglochin* or any other *Carex* was derived from within *Uncinia*. This analysis also rejects Savile and Calder's (1953) theory based on smut host-parasite data and their "phylogenetic principles" that those species of *Carex* subg. *Psyllophora* with a rachilla are a natural group, and it strongly excludes any lineage that involves *Uncinia* and *Carex* subg. *Vignea*.

There is, however, some congruence between this analysis and the speculations of Nelmes (1952) and Hamlin (1959). Because Nelmes (1952: 428) believed that the rachilla was "invariably absent" in the "2500 world-wide species" of *Carex* apart from subgenus *Psyllophora*, he thought that the rachilla's presence in subgenus *Psyllophora* species or their near relatives was "grounds alone" (Nelmes, 1952: 429) to suppose that their origins lay within *Uncinia*, *Kobresia*, or *Schoenoxiphium*. Hamlin's (1959) theory was essentially the same except that the "bulk" of subgenus *Psyllophora* and the genera *Kobresia*, *Uncinia*, and *Schoenoxiphium* were not derived from any extant group, but from a hypothetical uncinoid ancestor that retained the rachilla that was lost by the ancestor of *Carex* (i.e., subgenera *Carex*, *Vigneastra*, and *Vignea*). In this analysis, all of the taxa that Nelmes (1952) and Hamlin (1959) believed were derived from *Uncinia*, *Kobresia*, or *Schoenoxiphium* are found in either Clades A or B, and those they believed were derived from *Carex* subgenera *Carex* and *Vignea* are found in either Clades C or D, except the androgynous *C. leptalea* Wahlenb. (Clade A), which Nelmes considered a true *Carex* because it lacks a rachilla.

Nonetheless, it is difficult to give their theories much credibility, particularly in the case of Nelmes (1952: 431) where it is evident that *Uncinia* is not the "chief contributor" to *Carex* subg. *Psyllophora*. Moreover, both theories are based on a false premise; viz., the presumption that rachillae are "invariably absent" (Nelmes, 1952: 428) from subgenera *Carex*, *Vigneastra*, and *Vignea*. In reality, rachillae occur sporadically in all four of the subgenera in *Carex* (Snell, 1936; Svenson, 1972; Smith & Faulkner, 1976; Reznicek, 1990), and according to Snell (1936: 284) "nearly every species of *Carex* shows some remnant of the spikelet axis [i.e., rachilla] within the perigynium [i.e., utricle] at flowering time and even later." The conundrum of the rachilla is even further complicated by teratological specimens. In the case of the unispicate *C. phyllostachys* (section *Caryotheca*) and *C. backii* (section *Phyllostachyae*; Clades A and B), teratological proliferation of the rachilla leads to the production of androgynous spikes from basal utricles, a morphology that basically emulates the vigneastrian condition. It was largely for this reason that Kreczetovicz (1936) considered these taxa as the strongest evidence in favor of his theory that the majority of subgenus *Psyllophora* had evolved from the multispicate subgenus *Vigneastra* by rachilla reduction. As in Starr et al. (2004), the present analysis shows that the basal utricles in these taxa are not homologous to the lateral inflorescence units in subgenus *Vigneastra*. This is not entirely surprising since such teratological growth of lateral inflorescence units is in fact common throughout *Carex* (Smith & Faulkner, 1976;

Reznicek, 1990). It does, however, raise a potential systematic problem; viz., the possibility that teratological growth may become fixed. For example, Reznicek (1990) hypothesized that the androgynous *Vigneastra*-like lateral spikes of *C. baldensis* L. are potentially fixed outgrowths of the rachilla of a unispicate ancestor. This would indicate that the rachilla in one species' utricle may not be homologous to the rachilla in another, which can also be inferred from the conclusions of Smith and Faulkner (1976) and Timonen (1998) that the spikelets of *Kobresia* and *Schoenoxiphium* are not homologous to the spikelets in *Uncinia* and *Carex*. Although a more thorough study of rachilla morphology may yet prove rewarding at some taxonomic level in the Cariceae (Reznicek, 1990), the mere presence of rachillae is not a direct indication of phylogenetic relatedness or primitiveness (Reznicek, 1990; Starr et al., 1999).

THE INFRAGENERIC CLASSIFICATION OF *UNCINIA* AND THE CIRCUMSCRIPTION OF SECTION *UNCINIA*

This analysis is surprisingly consistent with previous infrageneric classifications of *Uncinia*. Clarke (1883) recognized two large sections, *Uncinia* and *Platyandrae*, and a monotypic section for *Carex microglochin* (*Pseudocarex* C. B. Clarke). Later authors, including Clarke (1908), excluded *C. microglochin* from the genus (e.g., Kükenthal, 1909), but they continued to use three principal groups by maintaining Clarke's (1883) sections *Uncinia* and *Platyandrae*, and by treating *U. kingii* as either a monotypic section (Hamlin, 1958) or subgenus (Kükenthal, 1909; Kukkonen, 1967). The present analysis is most consistent with the classification of Kükenthal (1909), who divided *Uncinia* into two subgenera, the first of which was composed of sections *Uncinia* and *Platyandrae* (subgenus *Eu-Uncinia*), while the second contained *U. kingii* (subgenus *Pseudocarex* Kük. nom. illeg. = subgenus *Hemihamatae*). This classification is preferable to that of Hamlin (1958), who recognized three sections (*Uncinia*, *Platyandrae*, and *Hemihamatae*) in that it acknowledges the strong body of evidence (Kukkonen, 1967; Meert & Goetghebeur, 1979; Reznicek, 1990) that *U. kingii* is unique (if treated as an *Uncinia*), while implying a sister group relationship.

The position of *Uncinia kingii* as sister to *Uncinia* s. str. raises, however, a difficult philosophical question as to how section *Uncinia* can be circumscribed from a morphological point of view. Clarke (1883) distinguished the two sections of *Uncinia* s. str. on the basis of whether the filaments were filiform (section *Uncinia*) or dilated (section *Platyandrae*), and on the uneven distribution of two further characters, hispid (all section *Platyandrae* spp.) versus glabrous (most section *Uncinia* spp.) utricles, and persistent (all section *Platyandrae* spp.) versus deciduous (most section *Uncinia* spp.) pistillate scales. *Uncinia kingii* with its filiform filaments, deciduous scales, and glabrous utricles cannot, on the basis of these characters, be separated from section *Uncinia*, and thus it is not surprising that Clarke (1883) placed it in that section and in its segregate section *Patagonicae* C. B. Clarke (Clarke, 1908). If *U. kingii* is in fact sister to *Uncinia* s. str. this would suggest that the characters used to circumscribe section *Uncinia* are plesiomorphic, and that section *Uncinia*, like *Uncinia* s.l., is a cryptic group (but see "Outgroups, rachilla theories, and the relationships of *Uncinia* and *Carex* sect. *Leucoglochin*"). Further support for this contention would appear to come from the position of section *Uncinia* series *Macrolepidae* (hispid utricles, persistent scales) within the section *Platyandrae* + series *Macrolepidae* clade, and by the clear monophyly of section *Platyandrae* (hispid utricles, persistent scales, and dilated filaments) itself. Similar trends in the generic-wide analysis of *Uncinia* by Starr (2001) and in the tribal analysis of Starr et al. (2004) suggest that "cryptic" clades may be common in the Cariceae, and that parallelisms and reversals in even the most important characters used for classification are widespread. This raises the prospect that a phylogenetic classification may be incompatible with the pragmatic need to create groups that can be easily diagnosed by traditional means (i.e., via a dissecting microscope), though a re-examination of morphology within a phylogenetic context may yet reveal previously unrecognized homologies (Starr et al., 2004).

TAXONOMY OF *CAREX MICROGLOCHIN*

In addition to its pivotal importance in the history of Cariceae classifications and phylogenetic theories, *Carex microglochin* is also interesting as one of only a handful of truly bipolar species (Constance et al., 1963; Moore & Chater, 1971). Although morphological (Boott, 1867; Kükenthal, 1909;

Kreczetovich, 1937) and anatomical (Kukkonen, 1970) differences have led authors to treat some South American plants as a separate variety or species, the high levels of infraspecific sequence divergence (10.2%) detected in this analysis and the placement of *C. microglochin* samples in separate clades are unexpected. This is especially true when all previous studies indicate that within species, variability is very low within the Cariceae (Starr et al., 1999, 2003) and angiosperms in general (Baldwin et al., 1995; Hershkovitz et al., 1999). Although the possibility of contamination cannot be entirely ruled out at the point of extraction, the fact that both individuals possessed unique and typical ITS and ETS 1f sequences from Europe and South America suggests that other evolutionary factors, such as hybridization, may be at work.

It is thought that bipolar distributions, like those of *Carex microglochin*, may have resulted during the late Pliocene or Pleistocene when cooler conditions at lower latitudes could have permitted temperate species the opportunity to disperse across tropical latitudes by following the Cordilleran system of North and South America (Constance et al., 1963; Moore & Chater, 1971). It is possible that the extreme differences between Northern and Southern hemisphere samples of *C. microglochin* could be explained by hybridization. Although this hypothesis needs to be confirmed, the exceptional geological and climatic events of the late Pliocene and Pleistocene have been linked to hybridization in several other groups (e.g., *Tellima grandiflora* (Pursh) Douglas, Soltis et al., 1991; *Quercus* L., Schaal et al., 1998; *Arabis* L., Dobeš et al., 2004).

Conclusions

As in previous Cariceae analyses, this study recovered four major clades in tribe Cariceae, suggesting that a general consensus among analyses is emerging. All studies indicate that *Uncinia* is monophyletic and part of a clade dominated by androgynous unispicate species of *Kobresia*, *Cymophyllus*, and *Carex* subgenera *Carex* and *Psyllophora* that also includes multispicate species of *Kobresia*. This clade is sister to a monophyletic group consisting of *Schoenoxiphium* and androgynous unispicate species of *Carex* subg. *Psyllophora*. The remaining species fall into two clades, one consisting of "typical" members of *Carex* subg. *Vignea* and a dioecious member of *Carex* subg. *Psyllophora* (*C. dioica*), and the second comprising "typical" members of *Carex* subgenera *Carex* and *Vigneastra*, and a dioecious member of *Carex* subg. *Psyllophora* (*C. scirpoidea*), that is sister to the remainder of the tribe.

Trees suggest that *Carex* is paraphyletic with respect to all other Cariceae genera. *Carex* subg. *Vignea* is monophyletic, but analyses suggest that *Carex* subg. *Psyllophora* is polyphyletic, and *Carex* subgenera *Vigneastra* and *Carex* should be merged. Analyses also reject the long-held hypotheses of a monophyletic *Schoenoxiphium* and *Kobresia* and a phylogenetic link between *Carex* subgenera *Vigneastra* and *Schoenoxiphium*. In addition, analyses continue to support a fundamental split among unispicate species. The dioecious members of *Carex* subg. *Psyllophora* are related to multispicate species in either *Carex* subgenera *Carex* or *Vignea*, while the androgynous unispicate members of *Carex* subgenera *Carex* and *Psyllophora* and the genera *Cymophyllus*, *Kobresia*, and *Uncinia* are variously placed in a clade that also contains multispicate species of *Schoenoxiphium* and *Kobresia*. *Cymophyllus* is sister to androgynous unispicate species in *Carex* subg. *Psyllophora*, and it cannot be morphologically separated from them.

Unfortunately, relationships among the major clades in Cariceae remain ambiguous, and statistical support for their monophyly continues to be poor. Although topological congruence would suggest that these clades are real, future increases in taxa and characters are needed to confirm these results.

The present analysis also indicates that *Uncinia* s. str. is sister to *U. kingii* and divided into two clades that roughly correspond to the traditional sections *Uncinia* and *Platyandrae*. This topology is surprisingly consistent with the classification of Kükenthal (1909), who divided *Uncinia* into two subgenera, the first of which was composed of sections *Uncinia* and *Platyandrae* (subgenus *Eu-Uncinia*), while the second contained *U. kingii* (subgenus *Pseudocarex* = subgenus *Hemihamatae*). The position of *U. kingii* as sister to *Uncinia* s. str. is unexpected as the compelling morphological and anatomical argument made by Reznicek (1990) would suggest that *U. kingii* is more closely related to *Carex microglochin* and its allies. The position of *U. kingii* as sister to *Uncinia* s. str. also poses a difficult practical and

philosophical problem as it creates two morphologically cryptic groups: (1) *U. kingii* + *Uncinia* s. str., which cannot be distinguished by any known synapomorphy, and (2) *Uncinia* sect. *Uncinia*, which cannot exclude *U. kingii* since it is circumscribed by plesiomorphic characters. Starr et al. (2004) has also detected such cryptic groups, although a re-examination of morphology within the context of recent phylogenies may reveal previously undetected synapomorphies.

Tree topologies do not support previous phylogenetic scenarios based on the reduction or proliferation of rachillae, although the groups detected in this analysis are most similar to those proposed by Nelmes (1952) and Hamlin (1959). Their evolutionary theories are difficult to accept, however, because they are based on the false premise that rachillae are invariably absent in *Carex* apart from subgenus *Psyllophora*, and the predicted origin of most subgenus *Psyllophora* species from *Uncinia* is unsupported by the data. It is clear that the reduction and/or proliferation of rachillae and spikes may occur in all Cariceae clades, but the mere presence of rachillae gives no indication of relatedness, evolutionary position, or the means by which a group originated.

Despite the seemingly strong morphological evidence that *Carex* sect. *Leucoglochin* is a homogeneous group, the present analysis suggests it is polyphyletic. Nonetheless, more data are needed to confirm this hypothesis as the present data cannot entirely reject a monophyletic section *Leucoglochin* or section *Leucoglochin* + *Uncinia* clade.

Previous authors have suggested that some South American individuals of *Carex microglochin* may constitute a separate variety or species. The Scottish and Ecuadorian samples of *C. microglochin* used in this analysis were placed in separate clades and possessed highly divergent but unique nrDNA spacer sequences. It is suggested that this may be due to hybridization, although further data are needed to confirm this hypothesis.

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Appendix 1

Classification and voucher data for Cariceae taxa used in ITS and ETS 1f analyses. Ingroup taxa are arranged in alphabetical order to series, with outgroup taxa placed last. Generic delimitation follows Kükenthal (1909) and Ball et al. (2002). Subgeneric circumscription adheres to Kükenthal (1909), Kukkonen (1967), and Zhang (2001), while sections follow Kükenthal (1909), Wheeler (1989), Egorova (1999), Dai and Liang (2000), Zhang (2001), and Ball and Reznicek (2002). The series of *Uncinia* are circumscribed as in Hamlin (1958, 1959) except for section *Platyandrae* ser. *Trichocarpae*, which includes *U. multifaria* Nees ex Boott (see Starr et al., 2003). Individuals sampled from the same species are numbered (1) and (2). Note that the voucher for *U. riparia* R. Br. could be one of three specimens (i.e., 1a, 1b, 1c), and that ITS and ETS 1f sequences of *U. triquetra* and *U. brevicaulis* Thouars were combined from two separate individuals. The type species for Cariceae genera (Goetghebeur, 1986; Nicolson, 1992) and *Carex* subgenera (Egorova, 1999) included in the analysis are marked respectively by (§) and (‡). GenBank numbers in parentheses represent sequences from Starr et al. (1999, 2003, 2004). Herbarium acronyms follow Holmgren et al. (1990).

Carex L.

subg. *Carex* sect. *Abditispicae* G. A. Wheeler, ***C. collumanthus*** (Steyerm.) L. E. Mora, COLOMBIA: Arauca, Sierra Nevada del Cocuy, *Cleef 8875* (NY) (AY241987, AY241988); sect. *Acrocystis* Dumort., ***C. albicans*** Willd., U.S.A.: Arkansas, Scott Co., *Ford 9440 & Naczi* (WIN) (AF027439, AF027478, AY241986); sect. *Depauperatae* Meinsh., ***C. depauperata*** Curtis ex With., UNITED KINGDOM: England, Surrey, *Rich 01* (OXF) (AY241984, AY241985); sect. *Laxiflorae* (Kunth) Mack., ***C. blanda*** Dewey, CANADA: Ontario, Peterborough Co., *Bakowsky 96-176* (WIN) (AF027445, AF027484, AY241983); sect. *Phacocystis* Dumort., ***C. nigra*** (L.) Reichard, FRANCE: Col du Luitel, *Playford 9807 et al.* (FHO) (AY241989, AY241990); sect. *Phyllostachyae* Tuck. ex Kük., ***C. backii*** Boott, CANADA: Ontario, Niagara R. M., *Ball s.n.* (WIN) (AF027411, AF027453, AY241968).

subg. *Psyllophora* (Degl.) Peterm. (= subg. *Primocarex* Kük.) sect. *Aciculares* (Kük.) G. A. Wheeler, ***C. acicularis*** Boott, NEW ZEALAND: Fiordland, Southland Land District, *Ford 113/98* (FHO) (AY242012, AY242013); ***C. vallis-pulchrae*** Phil., ARGENTINA: Tierra del Fuego, *Laegaard 13290* (AAU) (AY012619, AY012620); sect. *Caryotheca* V. I. Krecz. ex T. V. Egorova, ***C. phyllostachys*** C. A. Mey., TURKEY: Prov. Adana, Bahçe District, *Davis & Hedge* D. 26885 (BM 000059251) (AY242016, AY242017); sect. *Dornera* Heuff., ***C. nigricans*** C. A. Mey., CANA-

DA: British Columbia, Mount Revelstoke Natl. Park, *Ford 9720* (WIN) (AY242042, AY242043); ***C. pyrenaica*** Wahlenb., NEW ZEALAND: Fiordland, Southland Land District, *Ford 104/98* (FHO) AY244528, AY244529; sect. *Filifoliae* (Tuck.) Mack., ***C. filifolia*** Nutt., CANADA: Manitoba, Lauder Sand Hills, *Punter & Punter s.n.* (WIN) (AF027433, AF027473) AY244530; sect. *Firmiculmes* (Kük.) Mack., ***C. geyeri*** Boott, U.S.A.: Montana, Cascade Co., *Starr MT96039* (WIN) (AF027434, AF027474) AY244527; sect. *Junciformes* (Boeck.) Kük., ***C. aphylla*** Kunth, ARGENTINA: Prov. Río Negro, *Laegaard 13496* (AAU) (AY242014, AY242015); sect. *Leptocephalae* L. H. Bailey, ***C. leptalea*** Wahlenb., CANADA: Alberta, 2 km NE of Manly Corner, *Starr 96014 et al.* (WIN) (AY241979, AY241980); sect. *Leucoglochin* Dumort., ***C. microglochin*** Wahlenb., (1) ECUADOR: Prov. Chimborazo, *Molau, Eriksen & Klitgaard 2329* (GB) AY244519, AY244520, (2) UNITED KINGDOM: Scotland, Meall Greigh, *Starr 98017 & Scott* (FHO) AY244517, AY244518; ***C. parva*** Nees, CHINA: Yunnan, Diqing Prefecture, *Aldén et al. s.n., K.E.G. No. 1252* (E) AY244523, AY244524; ***C. pauciflora*** Lightf., FRANCE: Col du Luitel, *Playford 9806 et al.* (FHO) (AY242040, AY242041); sect. *Longespicatae* Kük., ***C. monostachya*** A. Rich., KENYA: *Muasya 1052* (K) (AY241977, AY241978); sect. *Nardinae* (Tuck.) Mack., ***C. nardina*** Fr., U.S.A.: Wyoming, Big Horn Co., *Starr et al. WY96134* (FHO) (AY241973, AY241974); sect. *Obtusatae* (Tuck.) Mack., ***C. obtusata*** Lilj., CANADA: Manitoba, Portage Sand Hills, *Ford 9601 et al.* (WIN) (AY241981, AY241982); sect. *Physoglochin* Dumort., ***C. dioica*** L., UNITED KINGDOM: Scotland, Ben Lawers Visitor's Centre, *Starr 98015 & Scott* (FHO) (AY241999, AY242000); sect. *Psyllophora* (Degl.) Koch, ***C. pulicaris***‡ L., UNITED KINGDOM: England, Yorkshire Dales Natl. Park, *Starr 98001 & Scott* (FHO) (AY242018, AY242019); sect. *Rupestres* (Tuck.) Meinsh., ***C. rupestris*** All., FRANCE: Col du Galibier, *Playford 9801 et al.* (FHO) AY244521, AY244522; sect. *Scirpinae* (Tuck.) Kük., ***C. scirpoidea*** Michx., CANADA: Alberta, Jasper Natl. Park, *Bayer AB-96010 et al.* (WIN) (AF027447, AF027486, AY241991).

subg. *Vignea* (P. Beauv. ex T. Lestib.) Peterm. sect. *Ammoglochin* Dumort., ***C. arenaria***‡ L., UNITED KINGDOM: Scotland, Lunan Bay Sand Dunes, *Starr 98020 & Scott* (FHO) (AY242003, AY242004); sect. *Curvulae* Tuck. ex Kük., ***C. curvula*** All., FRANCE: Col du Galibier, *Playford 9803 et al.* (FHO) (AY242030, AY242031); sect. *Deweyanae* (Tuck. ex Mack.) Mack., ***C. deweyana*** Schwein., CANADA: Alberta, Edmonton, *Starr* 96007 (WIN) (AF027437, AF027476, AY242007); sect. *Remotae* (Asch.) C. B. Clarke, ***C. remota*** L., UNITED KINGDOM: England, Yorkshire Dales Natl. Park, *Starr 98022 & Scott* (FHO) (AY242001, AY242002); sect. *Stellulatae* (Kunth) Christ, ***C. echinata*** Murray, UNITED KINGDOM: Scotland, Sròn Dha Murchdi, *Starr 98009 & Scott* (FHO) (AY242005, AY242006).

subg. *Vigneastra* (Tuck.) Kük. (= subg. *Indocarex* (Baill.) Kük.) sect. *Baccantes* (T. Koyama) P. C. Li, ***C. baccans*** Nees, TAIWAN: Wu Lai, Taipei, *Yen 078* (WTU) (AF027449, AF027488, AY241994); sect. *Indicae* Tuck., ***C. cruciata*** Wahlenb., MALAYSIA: Mulu Natl. Park, Sarawak, *Yen 075* (WTU) (AF027450, AF027489, AY241995); ***C. echinochloe*** Kunze, KENYA: *Muasya 1051* (K) (AY241992, AY241993); ***C. filicina*** Nees, TAIWAN: Yang Ming Shan Natl. Park, Da Tun Shan, *Yen 0076* (WTU) (AY241996, AY241997); sect. *Polystachyae* Tuck., ***C. polystachya*** Sw., BELIZE: Cayo District, *Jones 11275 & Wipff* (MICH) (AF027448, AF027487, AY241998).

Cymophyllus Mack.

C. fraserianus§ (Ker Gawl.) Kartesz & Gandhi, (1) U.S.A.: Tennessee, Blount Co., along rd. to Cades Cove, *Sharp s.n.* (cultivated at K), *Starr 98024 ex RBG Kew* (FHO) (AY241969, AY241970).

Kobresia Willd.

subg. *Compositae* (C. B. Clarke) Kukkonen, ***K. curticeps*** (C. B. Clarke) Kük., INDIA: Sikkim, East District, *Long & Noltie s.n., E.E.N.S. No. 73* (E) (AY242044, AY242045); ***K. laxa*** Nees, INDIA: Sikkim, North District, *Long & Noltie s.n., E.E.N.S. No. 211* (E) (AY241975, AY241976).

subg. *Kobresia* sect. *Hemicarex* (Benth.) C. B. Clarke, ***K. esenbeckii*** (Kunth) Noltie, INDIA: Sikkim, West District, Bikbari, *Long et al. s.n., E.S.I.K. No. 335* (E) (AY242032, AY242033); ***K. nepalensis*** (Nees) Kük., INDIA: Sikkim, North District, *Long & Noltie, E.E.N.S. No. 291* (E) (AY242034, AY242035); sect. *Kobresia*, ***K. myosuroides*** (Vill.) Fiori, FRANCE: Col du Galibier, *Playford 9804 et al.* (FHO) (AY242036, AY242037); ***K. schoenoides*** (C. A. Mey.) Steud., INDIA: Sikkim, West District, Chhoptha, *E.S.I.K. No. 647* (E) (AY242038, AY242039); ***K. simpliciuscula***§ (Wahlenb.) Mack., CANADA: British Columbia, Yoho Natl. Park, *Ford 9710* (FHO) (AY241971, AY241972).

Schoenoxiphium Nees

S. ecklonii Nees, SOUTH AFRICA: Cape Province, George-Knysna, *Baard 128* (PRE) (AY242024, AY242025); ***S. filiforme*** Kük., SOUTH AFRICA: Eastern Cape, Drakensbergs, *Phillipson 666* (PRE) (AY242020, AY242021); ***S. lanceum***§ (Thunb.) Kük., SOUTH AFRICA: Cape Province, Stellenbosch, *McDonald 829* (PRE) (AY242028, AY242029); ***S. lehmannii*** (Nees) Steud., SOUTH AFRICA: Natal

Province, Ngoye Forest Reserve, *Williams 1007* (PRE) (AY242026, AY242027); ***S. sparteum*** (Wahlenb.) C. B. Clarke, SOUTH AFRICA: Orange Free State, Ladybrand, *De Lange FA 57* (PRE) (AY242022, AY242023).

Uncinia Pers.

subg. *Eu-Uncinia* Kük. sect. *Platyandrae* C. B. Clarke ser. *Hamatae* Hamlin, ***U. hamata*** (Sw.) Urb., ECUADOR: Prov. Pichincha, N face of Pichincha, *Starr 99032 & Amigo* (FHO) (AY012664, AY012665); ser. *Macrotrichae* Hamlin, ***U. ecuadorensis*** G. A. Wheeler & Goetgh., ECUADOR: Prov. Cotocachi, S face of Nevado Cotacachi, *Starr 99020 & Amigo* (FHO) (AY012661, AY012662); ***U. erinacea*** (Cav.) Pers., CHILE: Isla Grande de Chiloé, Parque Nacional de Chiloé, *Vann 9804* (FHO) AY244531, AY244532; ser. *Trichocarpae* Hamlin, ***U. brevicaulis*** Thouars, (1) ST. HELENA: Tristan da Cunha, Inaccessible Island, *Christophersen 2473* (BM) AY244533, (2) ST. HELENA: Tristan da Cunha, above Burntwood, *Dickson 25* (AAS) AY244534; ***U. lacustris*** G. A. Wheeler, ECUADOR: Prov. Pichincha, Páramo de Guamani, *Laegaard 51887* (GENT) (AY012673, AY012674); ***U. multifaria*** Nees ex Boott, in Hook. f., CHILE: Isla Grande de Chiloé, P. N. de Chiloé, *Vann 9803* (FHO) (AY012667, AY012668); ***U. phleoides*** (Cav.) Pers., CHILE: Isla Grande de Chiloé, P. N. de Chiloé, *Vann 9801* (FHO) (AY012670, AY012671).

sect. *Uncinia* (= *Stenandrae* C. B. Clarke) ser. *Australes* Hamlin, ***U. clavata*** (Kük.) Hamlin, NEW ZEALAND: Westland Land District, Mt. Wilberg, *Wardle, Buxton & Ford s.n.* (CHR 500096) (AY012646, AY012647); ***U. ferruginea*** Boott, NEW ZEALAND: Wellington Land District, Ruahine Ranges, *Bellingham 786* (CHR) (AY012649, AY012650); ***U. uncinata***§ Kük., NEW ZEALAND: North Island, Auckland Ecological Region, *de Lange s.n.* (AK 226837) (AY242054), AY244543; ser. *Compactae* Hamlin, ***U. compacta*** R. Br., AUSTRALIA: Tasmania, SW Natl. Park, *Croft 10243 & Richardson* (CANB) AY244539, AY244540; ***U. flaccida*** S. T. Blake, AUSTRALIA: Australian Capital Territory, S slope of Mt. Murray, *Gilmour 6604* (CANB) (AY012643, AY012644); ***U. rupestris*** Raoul, NEW ZEALAND: Kokatahi River Catchment, spur W of a major confluence in Blue Duck Creek, *Bellingham 671* (CHR) (AY012640, AY012641); ser. *Graciles* Hamlin, ***U. banksii*** Boott, NEW ZEALAND: North Island, Auckland Ecological Region, *Cameron 7510* (AK) (AY012634, AY012635); ***U. subsacculata*** G. A. Wheeler & Goetgh., ECUADOR: Prov. Pichincha, N face of Pichincha, *Starr 99035 & Amigo* (FHO) (AY012652, AY012653); ***U. tenuis*** Poepp. ex Kunth, ECUADOR: Prov. Imbabura, Cerro Blanco, *Øllgaard 98225* (AAU) (AY012658, AY012659); ser. *Leptostachyae* Hamlin, ***U. leptostachya*** Raoul, NEW ZEALAND: Otago Land District, Otago Peninsula, *Enright s.n.* (CHR 505712) (AY012631, AY012632); ***U. scabra*** Boott, NEW ZEALAND: Wanganui, Waitotara River, *Ogle 2854* (CHR) (AY012625, AY012626); ser. *Macrolepidae* Hamlin, ***U. macrolepis*** Decne., ECUADOR: Prov. Pichincha/Napo, Volcan Antisana, *Starr 99028 & Amigo* (FHO) AY244535, AY244536; ***U. triquetra*** Kük., (1) ARGENTINA: Tierra del Fuego, Cerro Huehuepen, *Laegaard 13233* (AAU) AY244542, (2) CHILE: Laguna el Parrillar, Costa E., *Pisano 3.917* (RNG) AY244541; ser. *Ripariae* Hamlin, ***U. laxiflora*** Petrie, NEW ZEALAND: Wellington Land District, Ruahine Ranges, *Bellingham 789* (CHR) (AY012622, AY012623); ***U. riparia*** R. Br., (1a) AUSTRALIA: Tasmania, Lake St. Clair Natl. Park, *Wilson 8331* (K) AY244537, AY244538, (1b) AUSTRALIA: Tasmania, Pinnacle Mtn., *Hemsley 6652* (K), (1c) AUSTRALIA: Tasmania, 2 km E of Dee Lagoon Dam, *Wilson 6294* (K); ***U. rubra*** Boott, NEW ZEALAND: Cultivated. Provenance—Southland, Garvie Mountains, *Druce APD 1744* (CHR) (AY012628, AY012629).

subg. *Hemihamatae* (Hamlin) Kukkonen (= subg. *Pseudocarex* Kük., nom. illeg.), ***U. kingii*** Boott, CHILE: Isla Hoste, *Pisano 5530* (GH) AY244525, AY244526.

Outgroups

Eriophorum vaginatum L., UNITED KINGDOM: England, *Starr 98007 & Scott* (FHO) (AY242008, AY242009); ***Scirpus polystachyus*** F. Muell., AUSTRALIA: New South Wales, *Wilson s.n.* (MWC 5927) (K) (AY242010, AY242011).

Chapter 13

Towards a Revision of the Genus *Pleurostachys* (Cyperaceae): Preliminary Results

William Wayt Thomas and Marccus Alves

ABSTRACT Preliminary results of a study of the genus *Pleurostachys* Brongn. reveal 23 species, including five new to science. All species are Neotropical and 20 are endemic to Brazil's Atlantic coastal forest, with eight locally endemic. Preliminary cladistic analysis shows that the sectional circumscriptions used by Kükenthal in his 1952 revision of the genus will require modification.

KEY WORDS Cyperaceae, Neotropics, *Pleurostachys*, *Rhynchospora*, systematics.

Pleurostachys Brongn. is a small genus found exclusively in Neotropical forests. Kükenthal's 1952 monograph treated 30 species, 21 of which are endemic to Brazil's Atlantic coastal forest. Modern collections have greatly increased the number of specimens available for study, revealing the inadequacy of the material Kükenthal had at his disposal at that time.

The genus has long been considered closely related to *Rhynchospora* Vahl, and recent molecular studies (i.e., Muasya et al., 2000; Simpson et al., 2007) confirm this relationship. While there has been discussion as to whether or not *Pleurostachys* should be subsumed within *Rhynchospora*, most authors have maintained it as a separate genus closely allied to *Rhynchospora* (Boeckler, 1875; Clarke, 1908; Pfeiffer, 1925; Kükenthal, 1952; Koyama, 1961; Eiten, 1976; Goetghebeur, 1986, 1998; Bruhl, 1995; Dopchiz et al., 2000; Soros & Bruhl, 2000).

The aim of this study is to provide a checklist of the accepted names of *Pleurostachys* and a preliminary cladistic analysis based primarily on the characters used by Kükenthal (1952) to circumscribe sections in his revision of the genus.

Materials and Methods

Field studies carried out in Brazil's Atlantic coastal forest and the Amazon Basin from 1998–2002 increased the number of specimens available for our study. We also studied all available specimens of *Pleurostachys* in Brazilian herbaria as well as major U.S. and European herbaria (i.e., BHCB, BM, CVRD, FLOR, G, GOET, GUA, HB, HBR, HPZ, HUEFS, IAN, INPA, IPA, K, M, MBML, NY, P, PEUFR, R, RB, SP, SPF, UFP, W, and WU).

In order to evaluate the relationship of *Pleurostachys* to *Rhynchospora*, as well as the sectional circumscriptions of Kükenthal (1952), we studied all the species of *Pleurostachys* (except for *P. scaposa* C. B. Clarke, for which we have seen only the isosyntype fragments at MG and IAN, and *P. turbinata* (Nees) H. Pfeiff., for which the type has not yet been located).

Three species of *Rhynchospora* were chosen for phylogenetic comparisons and included in the analysis along with *Pleurostachys* (Table 1). *Rhynchospora argentea* Standl., *R. aristata* Boeckeler, and *R. kuntzei* C. B. Clarke were considered basal within *Rhynchospora* by Kükenthal (1949) and have some similarities to *Pleurostachys* (Table 2).

Of the 23 *Pleurostachys* spp. recognized in this study (Table 1), 19 were included in the analysis. Four species (*P. pearcei* C. B. Clarke, *P. scaposa*, *P. turbinata*, and *P.* sp. nov. 5) were excluded because of a lack of mature material.

The informative characters used were mostly derived from those used by Kükenthal (1952) in defining the genus *Pleurostachys* and delimiting its sections (Tables 2 and 3), generating a data set of 20 characters (Appendix 1, Table 4). Parsimony analysis was performed on the data set using NONA (Goloboff, 1999) with the MULTREES, tree bisection-reconnection (TBR), random addition sequence, and zero branch-length collapse options. WINCLADA (Nixon, 1999) was used to construct the trees and calculate jackknife indices (Farris, 1997) for support value of clades within trees.

Results and Discussion

We recognize 23 species of *Pleurostachys*, five of which are apparently new to science (Table 1). There are six names we have not yet been able to account for: *P. douglasii* C. B. Clarke, *P. extenuata* (Nees) Steud., *P. geraldiana* R. C. Davie, *P. longiradiata* Palla, *P. montana* Palla, and *P. turbinata*. The application of these names remains uncertain because type specimens have not yet been located and the protologues are not clear enough to enable us to either synonymize these names with earlier ones or recognize them as separate taxa. Most of the names, however, appear from their protologues to fall within our circumscriptions of species for which earlier names exist. Some of the species groups in Kükenthal's (1952) treatment represent extremes of variation of a single species—variation that he could not have assumed, based on the few specimens he had at his disposal.

Morphology

Pleurostachys and *Rhynchospora* have several characters in common. The spikelets are simple, the flowers are bisexual, and the achenes are lenticular, subtended by bristles, and capped with a persistent style base (Pfeiffer, 1925; Kükenthal, 1952; Eiten, 1976; Goetghebeur, 1998). *Pleurostachys*, however,

Table 1. Accepted species of *Pleurostachys* classified in sections based on the conspectus of Kükenthal (1952). Areas of occurrence as in Figure 1: area 1 (northern Amazon Basin, the Guianas, Venezuela, and eastern Colombia); area 2 (western Amazon Basin and eastern slopes of the Andes); area 3 (Atlantic coastal forest of northeastern Brazil); and area 4 (Atlantic coastal forest from Bahia south to Santa Catarina).

Sections of *Pleurostachys*	Studied species	Areas of occurrence
Scaposae Kük.	*P. scaposa* C. B. Clarke	1
Tenuiflorae H. Pfeiff.	*P. tenuiflora* Brongn.	4
Martianae H. Pfeiff.	*P. gaudichaudii* Brongn.	4
	P. peruviana C. B. Clarke	2
	P. turbinata (Nees) H. Pfeiff.	4
	P. urvillei Brongn.	4
	P. sp. 5 (new species)	4
Sparsiflorae Kük.	*P. macrantha* Kunth	4
	P. pearcei C. B. Clarke	2
	P. sparsiflora Kunth	1
Foliosae H. Pfeiff.	*P. foliosa* Kunth	4
Angustifoliae Kük.	*P. distichophylla* (Boeckeler) C. B. Clarke	4
	P. angustifolia Boeckeler	4
Millegranae (Benth. & Hook.) H. Pfeiff.	*P. beyrichii* (Nees) Steud.	4
	P. graminifolia Brongn.	4
	P. orbignyana Brongn.	4
	P. puberula Boeckeler	1, 2, 3, 4
	P. regnellii C. B. Clarke	
	P. stricta Kunth	4
	P. sp. 1–4 (new species)	4

is exclusively Neotropical and almost exclusively forest-loving.

Features that distinguish the two genera are listed in Table 2. The inflorescences of *Pleurostachys* spp. are axillary and usually lax and open, whereas in *Rhynchospora* they are terminal or axillary and morphologically diverse. The spikelet scales in *Rhynchospora* are spirally arranged, whereas in *Pleurostachys*, as in *Cyperus* L., they are distichous; the arrangement, however, is often obscured after the achenes enlarge. When the achene of *Pleurostachys* is viewed laterally, it is possible to see that the sides of the persistent style base are decurrent, running down the sides of the achene. In *Rhynchospora*, the style base may also be decurrent, but more often is discrete on the summit of the achene. The hypogynous bristles of *Pleurostachys* are usually flattened and often plumose toward the tip. In *Rhynchospora*, bristles may be absent or present, and if present, they are variable but seldom flattened. The bristles are usually retrorsely scabrous, occasionally entirely plumose, or plumose only at the base. They are rarely only apically plumose.

GEOGRAPHICAL DISTRIBUTION

Pleurostachys is found only in South American forests, and most species are found in the Brazilian Atlantic coastal forest (Table 1). Only two species (*P. pearcei* and *P. peruviana* C. B. Clarke) are non-Brazilian. *Pleurostachys pearcei* grows in Ecuador and Peru, and *P. peruviana* occurs in Bolivia and Peru. While most *Pleurostachys* spp. have restricted ranges, *P. puberula* Boeckeler is widely distributed in tropical American moist forests (Fig. 1, areas 1–4), occurring in the Guianas, Andean South America as far south as Bolivia, and Atlantic coastal Brazil. *Pleurostachys sparsiflora* Kunth and *P. scaposa* are found only in the northern Amazon Basin (Fig. 1, area 1). *Pleurostachys peruviana* and *P. pearcei* are restricted to the western Amazon Basin (Fig. 1, area 2). The remaining 18 species are restricted to the Atlantic coastal forest from Bahia

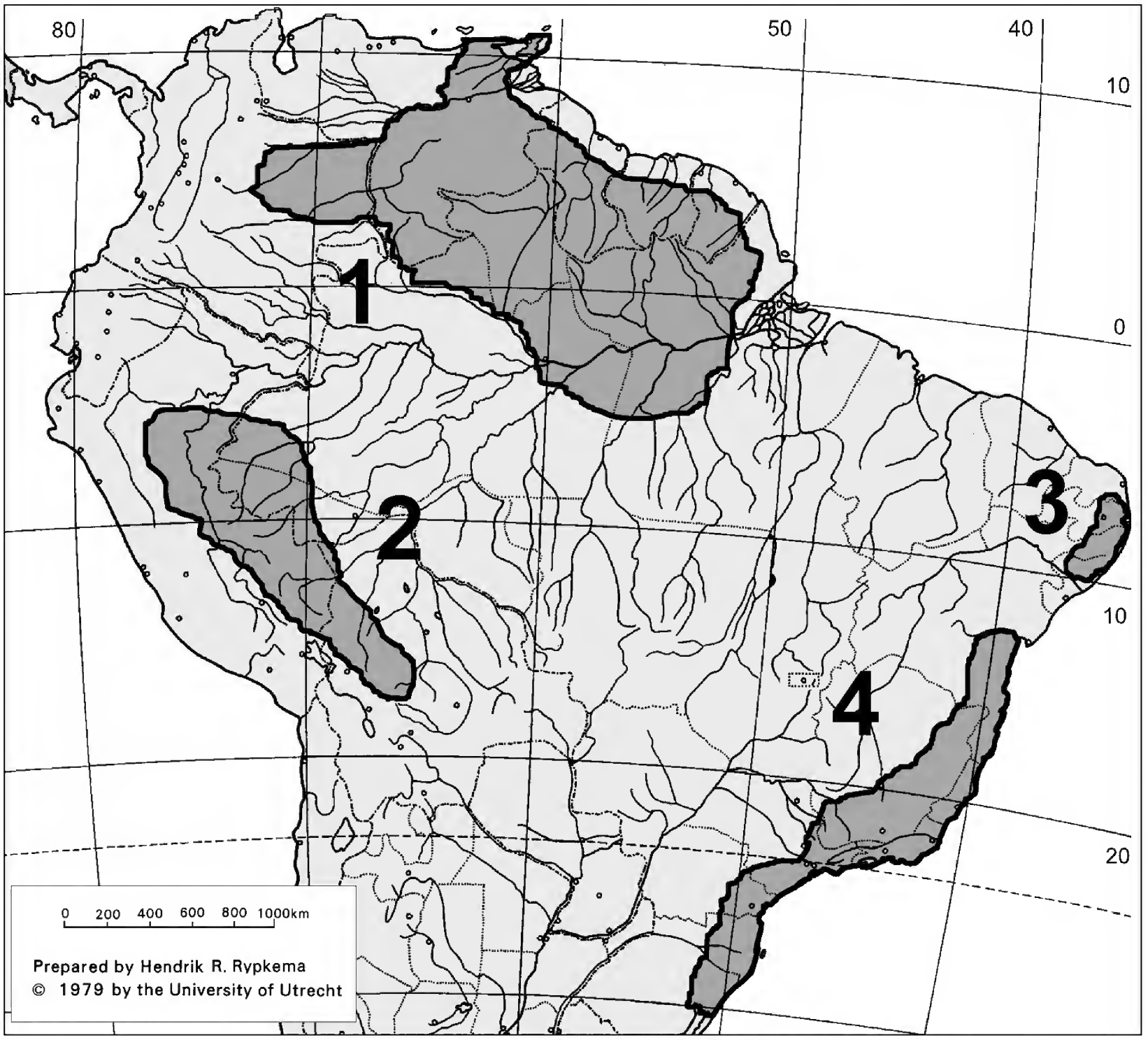

Figure 1. Geographical distribution of *Pleurostachys*. The numbered areas are: area 1 (northern Amazon Basin, the Guianas, Venezuela, and eastern Colombia); area 2 (western Amazon Basin and eastern slopes of the Andes); area 3 (Atlantic coastal forest of northeastern Brazil); and area 4 (Atlantic coastal forest from Bahia south to Santa Catarina). With the exception of the widely distributed *P. puberula* (found in all four areas), species are restricted to one of the four numbered areas, with the large majority (18 species) restricted to area 4. Two species are restricted to area 1 and two more species are restricted to area 2. Area 3 includes only the widely distributed *P. puberula*. No species are found outside the four shaded areas.

south to Santa Catarina (Fig. 1, area 4), with 10 species (*P. distichophylla* (Boeckeler) C. B. Clarke, *P. foliosa* Kunth, *P. gaudichaudii* Brongn., *P. macrantha* Kunth, *P. orbignyana* Brongn., *P. stricta* Kunth, *P. tenuiflora* Brongn., *P. urvillei* Brongn., and two new species) widely distributed and eight (*P. angustifolia* Boeckeler, *P. beyrichii* (Nees) Steud., *P. graminifolia* Brongn., *P. regnellii* C. B. Clarke, *P. turbinata*, and three new species) with narrow distributions. No species are found in the drier open cerrado or caatinga vegetation of the Brazilian Planalto. Thus, the genus is found in moist forests on all sides of the Planalto. This pattern is also seen in a number of genera of Cyperaceae, including *Calyptrocarya* Nees, *Diplacrum* R. Br. (Koyama, 1967), *Hypolytrum* Rich. (Alves et al., 2003), and some sections of *Rhynchospora* (Kükenthal, 1949, 1950, 1951; Thomas, 1994).

Table 2. Characteristics distinguishing the genera *Rhynchospora* and *Pleurostachys*.

Characters	*Rhynchospora* Vahl	*Pleurostachys* Brongn.
Spikelet scale arrangement	spirally arranged	distichously arranged
Bristle indument	variable, usually scabrous	usually distally plumose
Bristle cross-sectional shape	usually terete	usually flattened, at least basally
Achene/style base juncture	variable, usually not decurrent	usually decurrent
Inflorescence position	variable, terminal or axillary	axillary

Table 3. Characteristics of the sections of *Pleurostachys* as circumscribed by Kükenthal (1952).

Section	Culm leaves	Basal leaves	Leaf shape	Corymbs
Scaposae	absent	present	lanceolate	congested
Tenuiflorae	present	absent or bladeless	lanceolate	open, lax
Martianae	present	absent or bladeless	lanceolate	congested
Sparsiflorae	present	absent or bladeless	linear	open, very lax
Foliosae	present	absent or bladeless	linear	open, lax
Angustifoliae	present	absent or bladeless	linear	congested
Millegranae	present	present	linear	open to ± congested

SYSTEMATIC AND CLADISTIC ANALYSIS

Kükenthal (1952) divided *Pleurostachys* into seven sections, mostly characterized by the presence or absence of basal or cauline leaves and the size of the inflorescence and spikelets. The characters he used to distinguish and circumscribe the sections are listed in Table 3. As is discussed below, our preliminary cladistic analysis (Fig. 2) only partially supports the sectional circumscriptions used by Kükenthal.

Our analysis is preliminary and the number of morphological characters used is too low to provide good resolution. Nevertheless, the consensus tree (Fig. 2), with length (L) = 39, consistency index (CI) = 0.43, and retention index (RI) = 0.68, reflects some of the sectional circumscriptions we believe to be valid.

In all cases, *Rhynchospora* was distinguished from *Pleurostachys* (Node A) based on the characters listed above (Table 2) and used by Kükenthal (1952), Pfeiffer (1925), and others. Node B shows a polytomy that remains to be resolved; between nodes A and B, *Pleurostachys* "sp. nov. 1" is consistently shown to be the most basal species of *Pleurostachys*. While some of Kükenthal's sections (1952) do not hold up well (*Millegranae* (Benth. & Hook.) H. Pfeiff. [1] appears to be polyphyletic), others, such as *Sparsiflorae* Kük. (2, Node C), form a separate clade. Additional study will probably show that section *Foliosae* H. Pfeiff. (3) also forms a distinct clade. Node D is well resolved and groups together several sections of *Pleurostachys* (*Angustifoliae* Kük., *Foliosae*, *Martianae* H. Pfeiff., and *Scaposae* Kük.). The lack of resolution for these sections is probably due to low sample size and a low number of informative characters. The poor resolution may also reflect the possibility that some or all of these sections should be merged.

FUTURE RESEARCH

A completion of the revisionary research on *Pleurostachys* must be the first priority for research. This will require an intensive collecting effort, especially in the region from southern Bahia to Rio de Janeiro, to fully understand the distribution and mor-

Table 4. Morphological character matrix for *Pleurostachys* species (including four species new to science) and three outgroup *Rhynchospora* species (morphological characters and their states given in Appendix 1). – means that information is lacking or not applicable; * means that both character states apply.

Taxon	Character States																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Rhynchospora aristata	1	0	0	0	0	1	1	0	0	1	–	0	–	0	0	0	0	0	0	–
R. argentea	1	0	0	1	–	1	1	0	0	1	–	0	–	0	0	0	0	0	0	–
R. kuntzei	1	0	0	1	–	1	1	0	0	1	–	0	–	0	0	0	0	0	0	–
Pleurostachys sp–n 1	1	0	0	0	1	1	1	0	0	1	–	1	1	0	1	1	1	0	1	–
P. sp–n 2	1	0	0	0	0	1	1	1	0	0	1	1	0	1	0	1	1	1	–	0
P. sp–n 3	1	0	1	*	0	0	0	0	0	0	0	1	1	1	0	1	1	1	–	0
P. sp–n 4	1	0	0	0	0	1	0	*	0	0	1	1	1	1	0	1	0	1	–	1
P. angustifolia	1	1	0	0	0	0	0	0	0	0	0	1	0	1	*	1	1	1	–	0
P. beyrichii	1	0	0	0	0	*	1	0	0	0	0	1	1	1	0	1	1	1	–	0
P. bradei R. Gross	1	1	0	0	0	1	1	0	0	0	0	1	0	1	1	–	–	–	–	–
P. distichophylla	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	–	0
P. foliosa	1	1	0	0	0	1	1	0	0	0	0	1	1	1	0	1	1	1	–	0
P. gaudichaudii	1	1	0	1	–	1	0	0	0	0	*	1	1	1	0	1	1	1	–	1
P. graminifolia	1	0	0	0	0	1	0	0	0	0	*	1	0	1	0	1	0	0	1	–
P. macrantha	1	1	0	0	0	1	1	1	0	1	–	1	1	1	1	1	0	1	–	0
P. orbignyana	1	0	0	0	0	1	1	0	1	0	0	1	1	1	1	1	1	0	1	–
P. peruviana	1	1	0	1	–	0	0	0	0	0	0	1	0	0	1	1	1	0	1	–
P. puberula	1	0	0	0	0	1	1	0	1	0	0	1	1	1	0	1	1	1	–	0
P. regnellii	1	0	0	0	0	1	0	*	0	0	1	1	1	1	0	–	–	0	–	1
P. sellowii Kunth	1	1	0	0	0	1	1	0	0	0	0	1	1	1	1	1	1	1	–	0
P. sparsiflora	1	1	0	0	0	1	1	1	0	0	1	1	1	1	0	1	0	1	–	*
P. stricta	1	0	0	0	0	1	1	*	0	0	1	1	1	1	1	1	1	1	–	1
P. tenuiflora	1	1	0	1	–	1	1	0	0	0	1	1	0	1	0	1	1	1	–	0
P. undulatifolia R. Gross	0	0	0	1	–	0	0	0	0	0	0	1	0	1	0	1	1	1	–	1
P. urvillei	1	1	0	1	–	0	0	0	0	0	0	1	1	1	1	1	1	1	–	0

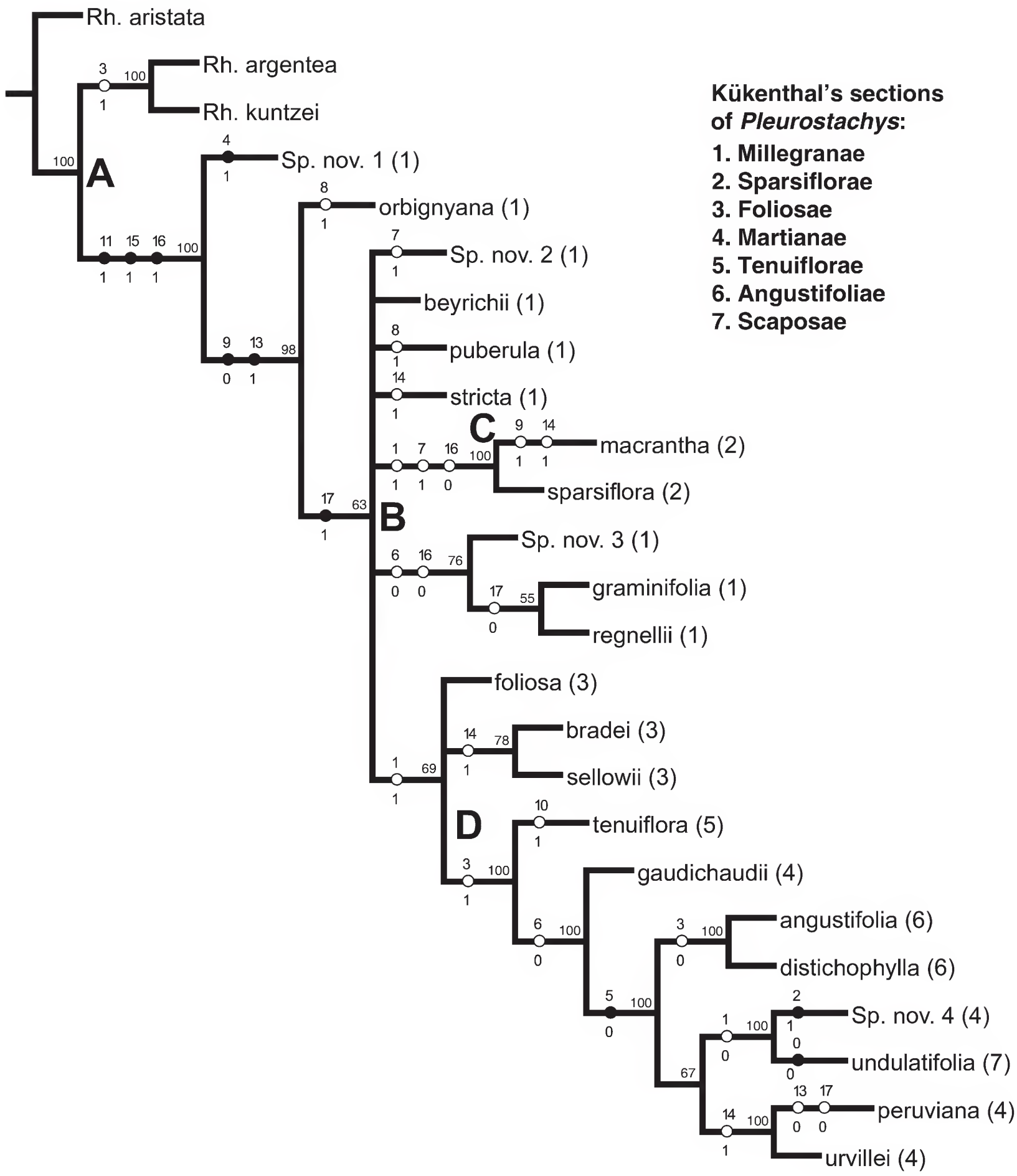

Figure 2. Consensus tree constructed using NONA (Goloboff, 1999) and WINCLADA (Nixon, 1999) of 19 species of *Pleurostachys* and three *Rhynchospora* species based on 14 morphological characters. While *R. aristata* was chosen to root the tree, two other *Rhynchospora* species, *R. argentea* and *R. kuntzei*, are also included to test the integrity of the *Pleurostachys* clade. Tree length (L) = 39, CI = 0.43, and RI = 0.68. The jackknife index (Farris, 1997) is given above each node. Kükenthal's (1952) sections are listed and numbered. The section to which each species pertains in Kükenthal's treatment is given in parentheses after the species name. Species not treated by Kükenthal are classified to section using his key to sections. Four nodes, marked with letters A–D, are discussed in the text.

phological variation of all taxa. Molecular analysis and an expanded morphological cladistic analysis can elucidate the relationship between *Pleurostachys* and *Rhynchospora*, the relationships among the species, and the distribution of species throughout tropical America.

Acknowledgments

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Appendix 1

Morphological characters and their states for *Pleurostachys* species (and some *Rhynchospora* species) listed in Table 4.

1. Culm leaves (leafy/leafless)
2. Basal blades (present/absent)
3. Blade length (long/short)
4. Blade shape (linear/lanceolate)
5. Linear leaf shape (linear/broadly linear)
6. Inflorescence axis length (short/elongate)
7. Inflorescence branching (few-branched/highly branched)
8. Spikelet grouping (clustered/single)

9. Clustered spikelet grouping (tightly clustered/loosely clustered)
10. Spikelet size (not large/large)
11. Non-large spikelet length (small/medium)
12. Spikelet scale disposition (spiral/distichous)
13. Distichous spikelet scale arrangement (partially distichous/completely distichous)
14. Bristle indument (scabrous/plumose, at least partially)
15. Disposition of bristle indument (uniform/alopecuroid)
16. Style base/achene summit juncture (not decurrent/decurrent)
17. Achene margin at style base (not sunken/sunken)
18. Length ratio style base:achene (< 2.5/> 2.5)
19. Low ratio style base:achene (< 1.5/ca. 2)
20. High ratio style base:achene (ca. 3/ca. 4)

Chapter 14

Cladistic Analysis in *Rhynchospora* Sect. *Pluriflorae* (Cyperaceae)

Ana Claudia Araújo, William Wayt Thomas, and Hilda M. Longhi-Wagner

ABSTRACT A cladistic analysis based on morphological characters was carried out on 28 species of *Rhynchospora* Vahl (Cyperaceae) and focused on the species of section *Pluriflorae* Kük. Forty-six characters were used including 10 leaf anatomical characters. The cladistic analysis produced 21 distinct most parsimonious trees of 219 steps. The strict consensus tree formed four clades, three of which represent the three subsections of section *Pluriflorae*. The fourth was formed mostly by species of section *Pauciflorae* Kük. and indicates that section *Pluriflorae* cannot be maintained as currently circumscribed.

KEY WORDS Cladistic analysis, Cyperaceae, Neotropics, *Rhynchospora*, section *Pluriflorae*.

The genus *Rhynchospora* Vahl comprises ca. 250 species (Thomas, 2004), mostly from the tropics and subtropics and with the highest diversity found in the Neotropics (Raynal, 1971; Koyama, 1972). Morphological diversity within *Rhynchospora* is high and inflorescences can range from large open panicles to single capitula, the latter often subtended by involucral bracts. Kükenthal (1949) divided *Rhynchospora* into two subgenera, the typical subgenus and subgenus *Haplostylis* (Nees & Meyen.) Benth. & Hook. f. Within *Haplostylis,* Kükenthal used inflorescence type as his primary division, separating all species with capitate inflorescences from the rest in his "Pars" *Capitatae.* He divided *Capitatae* into two sections, *Pluriflorae* Kük. and *Pauciflorae* Kük., distinguished on vegetative features and the number of flowers found in each spikelet.

While species of section *Pauciflorae* are found in the Americas, Africa, Asia, and Oceania (Kükenthal, 1949), species of section *Pluriflorae* are entirely Neotropical, with species distributed from Mexico to Uruguay and Argentina. Highest diversity of *Pluriflorae* is found in the Brazilian cerrados and campos rupestres (Araújo, 2001).

Within section *Pluriflorae*, Kükenthal (1949) recognized three subsections: subsection *Subebracteatae* Kük., with brown, scale-like involucral bracts shorter than the inflorescence; subsection *Brevibracteatae* Kük., with green, foliose involucral bracts two to three times longer than the inflorescence; and subsection *Longibracteatae* Kük., with green, foliose involucral bracts white at the base and at least three times longer than the inflorescence.

The objective of this study was to carry out a morphologically based phylogenetic analysis of *Rhynchospora* sect. *Pluriflorae*. Questions addressed included (1) Are sections *Pluriflorae* and *Pauciflorae* distinct? and (2) Are the three subsections within *Pluriflorae* distinct? The answer to these questions is not immediately obvious—a morphological analysis of section *Pluriflorae* (Araújo, 2001) revealed that some features traditionally used to characterize this section were not present in all its species (e.g., *R. hirta* (Nees) Boeck. has two to three flowers per spikelet; *R. armerioides* J. Presl & C. Presl, *R. exilis* Boeck., and *R. hirta* are caespitose with filiform culms and leaves). On the other hand, some of the characters that define *Pluriflorae* are present in some species of *Pauciflorae* (*R. capitata* (Kunth) Roem. & Schult. has a strong rhizome). Furthermore, *R. exilis* and *R. riedeliana* C. B. Clarke were poorly understood by Kükenthal (1949) and treated as incertae sedis.

Materials and Methods

Twenty-eight species were included in this analysis and are listed in Appendix 1. Forty-six characters—36 morphological and 10 leaf anatomical (13 of which were vegetative and 23 reproductive ones)—were included in the cladistic analysis (Table 1). Seventeen morphological characters were binary as were nine anatomical ones. The remaining characters were multistate. Some of the vegetative characters included in this analysis involved the base of the culm and inflorescence bracts. The reproductive characters analyzed mostly involved the hypogynous bristles, the persistent style base, and achene form, color, and indument. The leaf anatomical characters used include the presence or absence of Kranz anatomy and a hypoderm, and the shape of leaf transverse sections.

The data set was formatted (Table 2) and analyzed using WINCLADA 1.0.08 (Nixon, 2002). The parsimony analysis was performed using NONA 2.0 (Goloboff, 1999) with a heuristic search carried out using 1000 random addition sequences with 10 trees held during tree bisection-reconnection (TBR) swapping of each addition sequence (h/10;mult*1000).

Results

As a result of this analysis, 21 equally parsimonious trees were obtained, each with 219 steps, consistency index (CI) = 0.33, and retention index (RI) = 0.62. The strict consensus tree (Fig. 1) had 230 steps with CI = 0.32 and RI = 0.59. In it, the outgroup species, *Rhynchospora nervosa* (Vahl) Boeck., is distinct from the rest of the species, which are grouped into four clades.

The "consanguinea" clade (Fig. 1A) is characterized by species that lack hypogynous bristles and have small spikelets. Also, with the exception of *Rhynchospora longibracteata*, all have involucral bracts that are white at the base and persistent style bases that are circular in cross section. Even though involucral bracts with white bases appear to have evolved independently several times in *Rhyncho-*

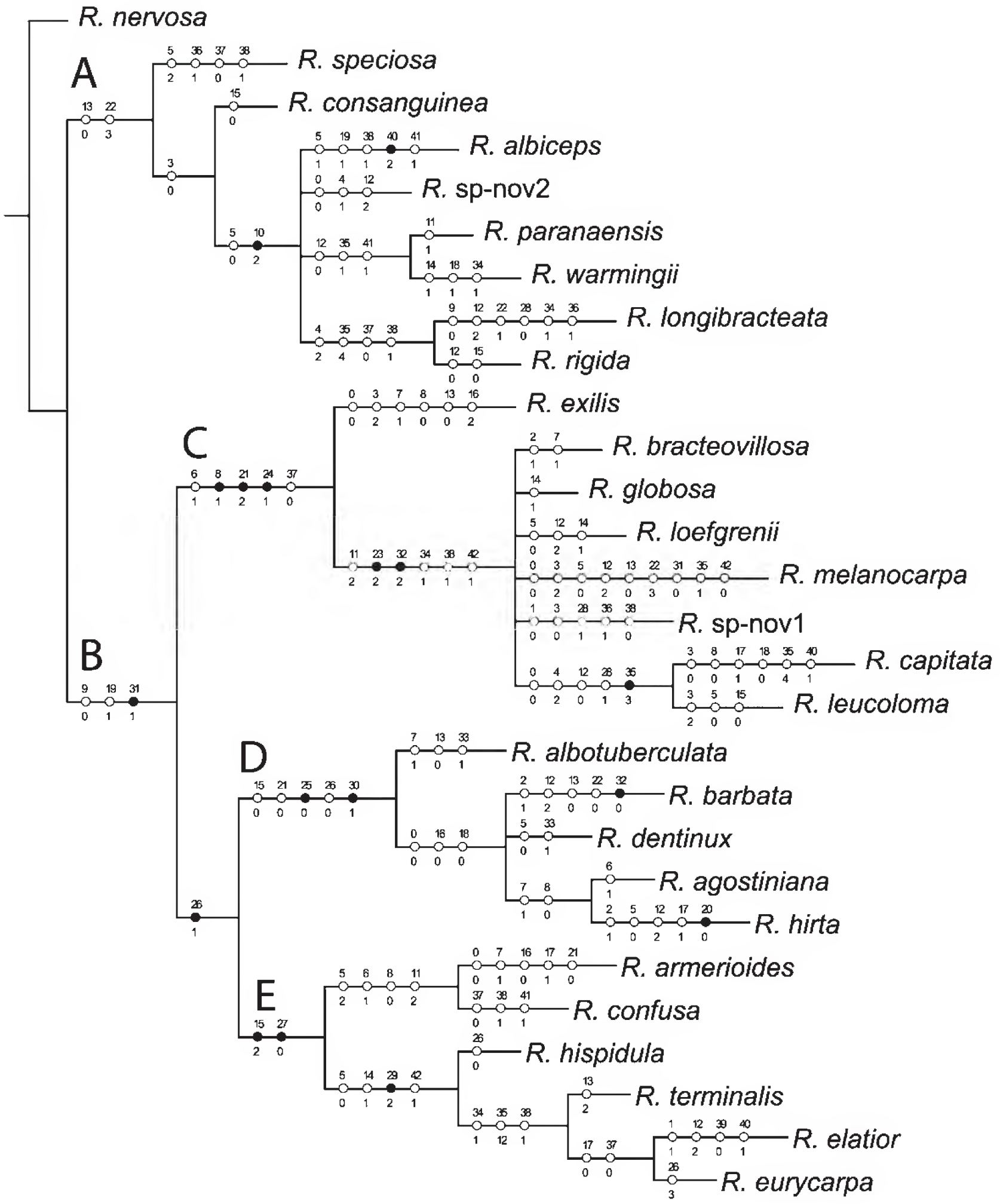

Figure 1. The strict consensus tree (230 steps; CI = 0.32; RI = 0.59) from a cladistic analysis based on morphological characters carried out on 28 species of *Rhynchospora* (Cyperaceae), focusing on the species of section *Pluriflorae*.

Table 1. Characters used in the analysis.

Code	Characters	State 0	State 1	State 2	State 3	State 4
0	Plant habit	caespitose	rhizomatous			
1	Plant base	sub-bulbiform	bulbiform			
2	Plant indument	glabrous	pilose			
3	Transverse section of culm	circular	trigonous	quadrangular		
4	Blade folding	flat	conduplicate	cylindrical		
5	Involucral bract number	up to 3	4 to 8	≥ 10		
6	Involucral bract appearance	leaf-like	scale-like			
7	Involucral bract margins	glabrous	ciliate			
8	Involucral bract consistency	membranous	chartaceous	coriaceous		
9	Base of involucral bract white	no	yes			
10	Form of base of white involucral bracts	lanceolate	ovate	widely ovate		
11	Involucral bract size	3× longer than inflorescence	2× longer than inflorescence	as long as inflorescence or less		
12	Inflorescence form	conical	hemispherical	globose		
13	Spikelet length	small (2–6.5 mm)	medium (7–9.5 mm)	large (> 10 mm)		
14	Spikelet compression	cylindrical	laterally compressed			
15	Spikelet shape	fusiform	ovoid	linear or lanceolate		
16	No. of flowers per spikelet	up to 3	5 to 10	> 10		
17	Scale color	white or dirty white	castaneous	ochraceous		
18	Scale consistency	membranous	chartaceous	cartilaginous		
19	Perianth bristle presence	absent	present			
20	Perianth bristle number	0	1	3 to 5	6	
21	Perianth bristle indument	pilose at base	scabrous	plumose		

22	Style base (transverse section)	flattened	lenticular	quadrangular	circular	
23	Style base form	triangular	conic	pyramidal		
24	Style base insertion	confluent	not confluent			
25	Style base edges	decurrent	not decurrent			
26	Achene form	narrowly obovate	oblong	obovate	widely obovate	ovate
27	Achene shape in transverse section	laterally compressed	biconvex			
28	Achene surface indument	absent	present			
29	Achene surface indument pattern	spinulose apically	tuberculate	papillose		
30	Achene margins	straight	incurved			
31	Achene margin ornamentation	absent	present			
32	Margin ornamentation consistency	membranous	cartilaginous	same as achene		
33	Margin ornamentation distribution	straight	denticulate			
34	Kranz anatomy pattern	absent	rhynchosporoid	chlorocyperoid		
35	Anatomy leaf in transverse section	"V" form	flat	crescentiform	triangular	circular
36	Anatomy leaf in transverse section	symmetrical	asymmetrical			
37	Bulliform cells	absent	present			
38	Hypodermis	absent	present			
39	Hypodermis pattern	uni- or biseriate	multiseriate			
40	Hypoderm form	continuous	discontinuous			
41	Sclerenchyma girders	on abaxial side	on both sides			
42	Idioblasts	absent	present			
43	Idioblast distribution	dispersed in mesophyll	on hypodermis			
44	Clefting of the style	deeply cleft	shallowly cleft			
45	No. of fruits per spikelet	1	1 to 4			

Table 2. Morphological character matrix for *Rhynchospora* species (characters and states given in Table 1). – means that information is lacking or not applicable.

Taxon	Character States																							
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
R. nervosa	1	0	1	1	0	1	0	1	2	1	0	0	0	1	0	0	2	0	0	0	–	–	0	0
R. agostiniana	0	–	0	0	0	1	1	1	0	–	–	1	1	1	1	0	0	2	0	1	1	0	1	0
R. albiceps	1	0	0	0	0	1	0	0	2	1	2	0	1	0	0	1	1	0	2	1	1	1	3	1
R. albotuberculata	1	0	0	1	0	1	0	1	2	0	–	1	1	0	0	0	1	2	2	1	2	0	1	0
R. armerioides	0	–	0	0	0	2	1	1	0	–	–	2	0	1,2	0	2	0	1	1	1	2	0	1	0
R. barbata	0	–	1	0	0	1	0	0	2	0	–	1	2	0	0	0	0	2	0	1	1	0	0	0
R. bracteovillosa	1	1	1	1	1	1	1	1	1	–	–	2	1	0,1	0	1	1	2	2	1	1	2	2	2
R. capitata	0	–	0	0	2	1	1	0	0	–	–	2	0	0,1	0	1	1	1	0	1	1	2	2	2
R. confusa	1	2	0	0	0,1	2	1	0	0	–	–	2	0	2	0	2	1	2	1	1	2	1	1	0
R. consanguinea	1	0	0	0	0	1,2	0	0	2	1	0	0	1	0	0	0	1	2	2	0,1	0,1,2	1	3	1
R. dentinux	0	–	0	0	0	0	0	0	2	0	–	1	1	1	1	0	0	2	0	1	2	0	1	0
R. elatior	1	1	0,1	0	0	0	0	0	2	0	–	1	2	1,2	1	2	1	0	2	1	2	1	1	0
R. eurycarpa	1	0	0	0	0	0	0	0	2	0	–	1	0	1	1	2	1	0	2	1	2	1	1	0
R. exilis	0	–	0	2	0	1	1	1	0	0	–	0	0	0	0	1	2	2	1	1	2	2	2	1
R. globosa	1	1	0	1	1	1	1	0	1	–	–	2	1	0,1	1	1	1	2	2	1	1	2	2	2
R. hirta	0	–	1	0	0	0	0	1	0	–	–	1	2	0,1	1	0	0	1	0	1	0	0	1	0
R. hispidula	1	–	0	0	0	0	0	0	2	0	–	1	0	1	1	2	1	2	2	1	2	1	1	0
R. leucoloma	0	–	0	2	2	0	1	0	1	–	–	2	0	1	0	0	1	2	2	1	1	2	2	2
R. loefgrenii	1	1	0	1	0	0	1	0	1	–	–	2	2	1	1	1	1	2	2	1	1	2	2	2
R. longibracteata	1	0	0	0	2	0	0	0	2	0	–	0	2	0	0	1	1	0	2	0	–	–	1	1
R. melanocarpa	0	–	0	2	0	0	1	0	1	–	–	2	2	0	0	1	1	2	2	1	1	2	3	2
R. paranaensis	1	–	0	0	0	0	0	0	2	1	2	1	0	0	0	1	1	2	2	0	–	–	3	1
R. rigida	1	0	0	0	2	0	0	0	2	1	1	0	0	0	0	0	1	2	2	0,1	0,1,2	1	3	1
R. sp. nov. 1	1	0	0	0	1	1	1	0	1	–	–	2	1	0,1	0	1	1	2	2	1	1	2	2	2
R. sp. nov. 2	0	–	0	0	1	0	0	0	2	1	2	0	2	0	0	1	1	0	2	0	–	–	3	1
R. speciosa	1	0	0	1	0	2	0	0	2	1	0	0	1	0	0	1	1	2	2	0	–	–	3	1
R. terminalis	1	0	0,1	0	0	0	0	0	2	0	–	1	1	2	1	2	1	2	2	1	2	1	1	0
R. warmingii	1	0	0	0	0	0	0	0	2	1	2	0	0	0	1	1	1	2	1	0	–	–	3	1

Taxon	Character States																					
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
R. nervosa	0	1	4	1	0	–	0	0	–	–	0	0	0	1	0	–	–	0	0	–	0	1
R. agostiniana	0	0	0	1	0	–	1	1	1	0	–	–	–	–	–	–	–	–	–	–	1	0
R. albiceps	0	1	2	1	1	1	0	0	–	–	0	0	0	1	1	1	2	1	0	–	1	0
R. albotuberculata	0	0	0	1	0	–	1	1	1	1	–	–	–	–	–	–	–	–	–	–	1	0
R. armerioides	0	1	1	0	1	0	0	1	1	0	0	0	0	1	0	–	–	0	0	–	1	0
R. barbata	0	0	0	1	0	–	1	1	0	0	0	0	0	1	0	–	–	0	0	–	1	0
R. bracteovillosa	1	–	2	1	0	–	0	1	2	0	1	0	0	0	1	1	0	0	1	–	1	0
R. capitata	1	–	2	1	1	0	0	1	2	0	1	4	0	0	1	1	1	0	1	0	1	0
R. confusa	0	1	1	0	0	–	0	1	1	0	0	0	0	0	1	1	1	1	0	–	1	0
R. consanguinea	0	1	2	1	1	1	0	0	–	–	0	0	0	1	0	–	–	0	0	–	1	0
R. dentinux	0	0	0	1	1	0	1	1	1	1	–	–	–	–	–	–	–	–	–	–	1	0
R. elatior	0	1	1	0	1	2	0	1	1	0	1	1	0	0	1	0	1	0	1	1	1	0
R. eurycarpa	0	1	3	0	1	2	0	1	1	0	1	2	0	0	1	1	0	0	1	0	1	0
R. exilis	1	1	2	1	1	0	0	1	1	0	0	0	–	0	0	–	0,2	0	0	–	1	0
R. globosa	1	–	2	1	0	–	0	1	2	0	1	0,3	0	0	1	1	0	0	1	0	1	0
R. hirta	0	0	0	1	1	0	1	1	1	0	2	1	0	1	1	0	0	0	1	1	1	0
R. hispidula	0	1	0	0	1	2	0	1	1	0	0	0	0	1	0	–	–	0	1	1	1	0
R. leucoloma	1	–	2	1	1	0	0	1	2	0	1	3	0	0	1	1	0	0	1	0	1	0
R. loefgrenii	1	–	2	1	0	–	0	1	2	0	1	0	0	0	1	1	0	0	1	0	1	0
R. longibracteata	0	1	2	1	0	–	0	0	–	–	1	4	1	0	1	1	0	0	0	–	1	0
R. melanocarpa	1	–	2	1	0	–	0	0	–	–	1	1	0	0	1	1	0	0	0	–	1	0
R. paranaensis	0	1	2	1	1	1	0	0	–	–	0	1	0	1	0	–	–	1	0	–	1	0
R. rigida	0	1	2	1	1	1	0	0	–	–	0	4	0	0	1	1	0	0	0	–	1	0
R. sp. nov. 1	1	–	2	1	1	0	0	1	2	0	1	0	1	0	0	1	–	0	1	0	1	0
R. sp. nov. 2	0	1	2	1	1	1	0	0	–	–	0	0	0	1	0	–	–	0	0	–	1	0
R. speciosa	0	1	2	1	1	1	0	0	–	–	0	0	1	0	1	1	0	0	0	–	1	0
R. terminalis	0	1	1	0	1	2	0	1	1	0	1	2	0	1	1	1	0	0	1	0	1	0
R. warmingii	0	1	2	1	1	1	0	0	–	–	1	1	0	1	0	–	–	1	0	–	1	0

spora (Thomas, 1984), this feature is one of the defining synapomorphies for this clade.

The remaining species (Fig. 1B) are distinguished by the presence of achene margin ornamentation, involucral bracts without a white base, and the presence of hypogynous bristles. The "globosa" clade (Fig. 1C) comprises a group of species that have scale-like, chartaceous involucral bracts, plumose (at least basally) hypogynous bristles, and an absence of bulliform cells in the leaves.

The last two clades are characterized by achenes that are narrowly obovate or oblong in outline. The "barbata" clade (Fig. 1D) is characterized by an incurved achene margin, a decurrent style base edge, basally pilose hypogynous bristles, and fusiform spikelets. The "elatior" clade (Fig. 1E) comprises species that have lanceolate spikelets and laterally compressed achenes.

Discussion

Of the species of *Rhynchospora* selected for this study, 23 were classified using Kükenthal's (1949) criteria as belonging to section *Pluriflorae* and five were classified as belonging to other sections (Appendix 1), thereby functioning as a test of the integrity of *Pluriflorae*. In Figure 1, clades C and D both include species of section *Pauciflorae*. These two clades are part of a larger clade B, which is sister to clade A, comprised entirely of species of section *Pluriflorae*. Therefore, the *Pluriflorae* as circumscribed by Kükenthal are polyphyletic.

Nevertheless, at the subsectional level, there is considerable agreement between the cladistic analysis and Kükenthal's (1949) classification. Clade A, the "consanguinea" clade, of Figure 1 comprises all the studied species of subsection *Longibracteatae* including *Rhynchospora longibracteata*, which Thomas (1997) included in a new section, *Rigidifolia* W. W. Thomas.

Clade C, the "globosa" clade, with the exception of *Rhynchospora capitata*, is composed entirely of species of subsection *Subebracteatae*. Two species classified by Kükenthal as members of this subsection, *R. hirta* and *R. armerioides*, are, however, found elsewhere, in clades D and E. Clade E, the "elatior" clade, is also reasonably consistent with Kükenthal's classification. With the exception of *R. armerioides*, it is made up only of species of section *Brevibracteatae*.

Clade D, the "barbata" clade, is the most heterogeneous, with one species each classified by Kükenthal as *Subebracteatae* or *Brevibracteatae*. The remaining three species are all classified as members of section *Pauciflorae*.

The three subsections of Kükenthal's (1949) section *Pluriflorae* appear to be supported by morphological evidence as clades A, C, and E, even though a few species seem to be misplaced. The emergence of section *Pauciflorae* (clade D) as sister to subsection *Brevibracteatae* (clade E) raises the possibility that sections *Pauciflorae* and *Pluriflorae* should be joined. Future research, especially molecular analyses (Araújo & Thomas, 2005; Thomas et al., 2005), should clarify some of the possible outcomes suggested here.

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Appendix 1

The species used in the analysis as classified to section and subsection by Kükenthal (1949, 1950, 1951). Species described since Kükenthal's treatment or for which he had insufficient material are classified according to his criteria and marked with an *.

OUTGROUP

Subgenus *Rhynchospora*: *R. nervosa* (Vahl) Boeck.

INGROUP

Subgenus *Haplostylis*:

Section *Pauciflorae*: *R. agostiniana* T. Koyama; *R. barbata* (Vahl) Kunth; *R. capitata* (Kunth) Roem. & Schult.; *R. dentinux* C. B. Clarke.

Section *Pluriflorae*:

Subsection *Subebracteatae*: *R. armerioides* J. Presl & C. Presl, **R. bracteovillosa* A. C. Araujo & W. W. Thomas, **R. exilis* Boeck., *R. globosa* (Kunth) Roem. & Schult., *R. hirta* (Nees) Boeck.; **R. leucoloma* A. C. Araujo & Longhi-Wagner, *R. loefgrenii* Boeck., **R. melanocarpa* A. C. Araujo & W. W. Thomas, and **R.* sp. 1.

Subsection *Brevibracteatae*: *R. albotuberculata* Kük.; *R. confusa* F. Ballard; *R. elatior* Kunth; **R. eurycarpa* A. C. Araujo & Longhi-Wagner; *R. hispidula* Griseb. (= *R. grisebachii* Boeck.); *R. terminalis* (Nees) Steud.

Subsection *Longibracteatae*: *R. albiceps* Kunth.; *R. consanguinea* (Kunth) Boeck.; *R. longibracteata* Boeck.; **R. paranaensis* A. C. Araujo & W. W. Thomas; *R. rigida* (Kunth) Boeck.; **R.* sp. 2; *R. speciosa* (Kunth) Boeck.; *R. warmingii* Boeck.

Unclassified species: *Rhynchospora exilis* Boeck. and *R. riedeliana* C. B. Clarke were listed by Kükenthal (1949) as incertae sedis within section *Pluriflorae*. While *R. exilis* is treated here as subsection *Subebracteatae*, *R. riedeliana* is excluded because molecular and morphological analyses by Araújo et al. (unpublished data) demonstrate that this species is best placed in Kükenthal's *Anthelatae* group.

Taxonomic Index

Abildgaardia, 22, 23, 30, 31, 54, 106, 108
  ovata, 30, 77
Acer
  rubrum, 133, 139, 140, 141
Actinoscirpus, 3, 23
  grossus, 8
Afrotrilepis, 3, 24
  pilosa, 6, 10
Amblystegiaceae, 147
Amelanchier
  arborea, 133, 139
Andromeda, 178
  glaucophylla, 147
Androtrichum, 24
Anosporum, 23, 24
Arabis, 261
Arachis
  hypogaea, 35
Ascolepis, 3, 22
Asteraceae, 104

Beta
  vulgaris, 36
Betula
  glandulosa, 164, 185
  pumila, 147
Blysmopsis, 165
Bolboschoenus, 10, 22, 23, 26, 30–31, 53, 54, 106, 109
  affinis, 77
  caldwellii, 77
  fluviatilis, 31, 77
  glaucus, 68
  maritimus, 12, 30, 31, 68, 77
    subsp. *paludosus*, 68
  novae-angliae, 109
  paludosus, 10
  planiculmis, 77
  robustus, 27, 46, 68, 113
  yagara, 10
Bulbostylis, 3, 23, 30, 53, 54, 106, 108, 109
  barbata, 31, 77
  capillaris, 31, 77
  ciliatifolia, 31, 77
    var. *ciliatifolia*, 110
  densa, 77
  filamentosa, 77
  hispidula, 77
    subsp. *pyriformis*, 77
  humilis, 68, 77
  puberula, 77
  stenophylla, 112
  striatella, 68
  warei, 110
Calyptrocarya, 272
Capsicum
  annuum, 24
Carex, 1, 3, 4, 5, 6, 8, 22, 23, 25, 30, 31, 53, 54, 105, 106, 108, 109, 119, 120, 122, 128, 130, 146, 147, 148, 152, 159, 163, 165–167, 176, 178, 187–195, 210, 212, 215, 216, 227, 228, 237, 240, 243, 244, 245, 246, 247, 248, 251, 252, 258, 259, 260
  abrupta, 190, 204
  abscondita, 122–124
  acicularis, 253, 265
  acuta, 68, 77, 215, 216, 218, 220, 221, 222, 223, 224
  acutiformis, 68
  adelostoma, 163, 168, 170, 172, 174, 183
  adusta, 170, 172, 182, 206
  alata, 204
  alba, 68
  albicans, 265
    var. *australis*, 124
  albolutescens, 77, 124, 128, 204
  albula, 68, 77
  albursina, 105–106
  alternifolius, 3, 4
  antarctogena, 167
  aphylla, 253, 266
  appressa, 68
  aquatilis, 33, 78, 148, 149, 150, 153, 155, 157, 158, 159, 163, 177, 185, 215, 216, 219, 220, 221, 223, 224
    subsp. *stans*, 168
    var. *aquatilis*, 169, 171, 172, 183
    var. *minor*, 168
    var. *stans*, 177
    var. *substricta*, 219, 220, 224
  arapahoensis, 206
  arcta, 169, 172, 182
  arctata, 190
  arctogena, 163, 167, 176, 188, 190
  arenaria, 68, 188, 190, 193, 266
  argyrantha, 206
  atherodes, 33, 78
  athrostachya, 199, 204, 211
  atlantica, 128
    subsp. *capillacea*, 124
  atrata, 68, 163, 174
  atratiformis, 163, 169, 172, 174, 183
  atrofusca, 168, 169, 170, 184
  aurea, 107, 169, 170, 183, 216
  aureolensis, 33, 78, 113, 124
  australis, 128
  austrina, 68, 124
  baccans, 27, 68, 78, 253, 266
  backii, 191, 227, 228, 229, 233, 234, 235, 236, 237, 239, 240, 254, 259, 265
    var. *subrostrata*, 233
  baldensis, 68, 260
  baltzellii, 68, 111
  basiantha, 124, 191, 227, 228, 229, 230, 231, 239
  bebbii, 205
  bella, 216, 219, 220
  berggreni, 68
  bicknellii
    var. *bicknellii*, 205
  bicolor, 169, 170, 172, 216, 219
  bigelowii, 163, 169, 171, 173, 190, 191, 215, 216, 219, 220, 221, 223
    subsp. *bigelowii*, 169, 170, 171, 172, 183
  biwensis, 78
  blanda, 32, 78, 124, 265
  bohemica, 199, 204, 209, 211
  bonariensis, 78
  bonplandii, 204
  breviculmis, 78, 190
  brevicuspis, 78
  brevior, 68, 205
  brizoides, 78, 198, 202, 210
  bromoides
    subsp. *bromoides*, 124
  brongniartii, 78
  brunnea, 68
  brunnescens, 149, 169, 171, 172, 176
    subsp. *brunnescens*, 172, 182
    subsp. *sphaerostachya*, 176
  buchananii, 68, 78
  bulbostylis, 124, 126
  buxbaumii, 163, 169, 172, 174, 183
  calcifugens, 109
  canescens, 78, 149, 150, 155, 156, 159, 163, 167, 168, 172, 176, 203
    subsp. *canescens*, 165, 167, 169, 172, 175, 176, 182, 185
    subsp. *disjuncta*, 165, 170, 172, 175, 176, 182
    var. *robustior*, 167
    var. *subloliacea*, 176
  capillaris, 149, 163, 169, 170,

Carex (continued)
172, 174, 183
capitata, 163, 167, 168, 169, 172, 176, 184, 190, 202
var. *arctogena*, 167
var. *capitata*, 167
caroliniana, 124
caryophyllea, 68
castanea, 170, 171, 172, 173, 183, 190
cephaloidea, 203
cephalophora, 32, 123, 124, 203
cernua, 12
cherokeensis, 32, 68, 78, 124, 125
chordorrhiza, 149, 150, 155, 158, 169, 170, 172, 182, 198, 200, 201, 202, 209
collumanthus, 265
comans, 27, 68, 78
comosa, 33, 78, 130
complanata, 124
concinna, 170, 172, 173, 184
conica, 68
conoidea, 170, 172, 183
constanceana, 201, 207
cordillerana, 227, 228, 233, 234, 235, 236, 237, 239
coriacca, 78
corrugata, 124–125
crawei, 105–106, 107
crawfordii, 68, 170, 172, 182, 201, 205
crebriflora, 126
crinita, 68, 126, 188
var. *crinita*, 190
cristatella, 201, 207
cruciata, 266
crus-corvi, 126
cuchumatanensis, 216
cumulata, 204
curaica, 203
curta
var. *curta*, 167
var. *robustior*, 167
curvula, 68, 198, 254, 256, 266
dasycarpa, 110
davisii, 107
davyi, 201, 207
debilis, 128, 130
var. *debilis*, 126
decidua, 216
decomposita, 119, 120, 126, 130
deflexa
var. *deflexa*, 169, 172, 184
depauperata, 265
devia, 68
deweyana, 69, 266
subsp. *deweyana*, 202
diandra, 31, 53, 69, 149, 169, 170, 182
dietrichiae, 78
digitalis, 110
var. *digitalis*, 126
var. *floridana*, 110, 126
var. *macropoda*, 126
digitata, 69
diluta, 53
dimorpholepis, 78
dioica, 254, 255, 256, 261, 266
dipsacea, 69
dispalata, 78
disperma, 149, 150, 153, 157, 158, 159, 169, 172, 182
dissita, 69
disticha, 78
divisa, 53, 78
divulsa, 69, 78
dolichostachya, 69
donnell-smithii, 216, 219, 220
ebenea, 204
eburnea, 69, 107, 170, 172, 173, 184
echinata, 266
subsp. *echinata*, 169, 171, 172, 182
echinochloe, 266
egglestonii, 205
elata, 69, 216, 218, 224
eleusinoides, 215, 218, 221, 223, 224
elliottii, 110
ensifolia
subsp. *arctisibirica*, 191
eurycarpa, 78
exilis, 105–106, 107, 149, 150, 153, 169, 171, 182
×*exsalina*, 183
exserta, 69
fedia, 78
festucacea, 125, 126, 205
feta, 206
filicina, 266
filifolia, 238, 249–250, 251, 253, 254, 256, 266
var. *erostrata*, 8
firma, 69
×*firmior*, 183
fissa
var. *aristata*, 110
flacca, 69
flaccosperma, 69, 126, 127
flagellifera, 69, 78
flava, 69, 107, 190
×*flavicans*, 163, 165, 173, 177–178, 183, 185
floridana, 110, 128
foenea, 169, 172, 182, 206
foliosa, 79
folliculata, 128
var. *australis*, 128
fracta, 207
frankii, 33, 79, 124
fuliginosa, 168, 169, 170, 172, 184
gallaecica, 69
garberi, 169, 170, 172, 183
gaudichaudiana, 69, 218, 221, 224
gayana, 79
geyeri, 69, 238, 266
gholsonii, 110
gigantea, 113, 126
glacialis, 169, 172, 184
glareosa, 174
subsp. *glareosa*, 169, 170, 182
glauca, 79
glaucescens, 33, 79, 112, 126
glaucodea, 126
godfreyi, 110
gracilior, 204
gracillima, 202
graeffeana, 79
×*grantii*, 183
granularis, 126
gravida, 203
grayi, 69
gynandra, 190
gynocrates, 149, 150, 153, 155, 157, 158, 159, 169, 170, 172, 177, 182
gynodynama, 190
hachijoensis, 69
harfordii, 190, 204
hartmanii, 174
haydeniana, 204
haydenii, 202
heleonastes, 149, 150, 153, 163, 169, 171, 174, 182
hermannii, 218
heterostachya, 33, 79
hirta, 69, 79
hirtissima, 188, 190
hitchcockiana, 107
holostoma, 169, 170, 172, 183
hondoensis, 190
hoodii, 69, 203
hormathodes, 206
howei, 124
hubbardii, 69
hudsonii, 79

Carex (continued)
humilis, 69, 188
var. *nana*, 190
hyalina, 124–125, 126, 128, 205
hyalinolepis, 126
illota, 197, 198, 199, 200, 201, 204, 209
integra, 190, 205
interior, 150, 158, 159, 170, 182, 203
interjecta, 207
intumescens, 69, 126
inversa, 69, 79, 198
iynx, 79
jamesii, 188, 191, 227, 228, 229, 230, 231, 232, 233, 234, 239, 240
jemtlandica, 190
joorii, 126–128, 128
juniperorum, 191, 227, 230, 231, 232, 233, 239
kaloides, 69
kingii, 244, 247
×*knieskernii*, 188, 190
kobomugi, 32, 42, 69, 79
krausei, 163, 170, 174, 183
lachenalii, 169, 172, 174, 182
lacustris, 33, 79
lagunensis, 207
×*langeana*, 176–177, 182
lanuginosa, 32
lapponica, 163, 165, 168, 170, 172, 173, 175, 176, 178, 182, 185
lasiocarpa, 33, 79, 190
latebracteata, 191, 227, 228, 237, 238, 239, 240
leavenworthii, 32, 79, 128
lemanniana, 216, 219, 220
lenticularis, 215, 216, 218, 221, 223, 224
var. *impressa*, 218, 220, 223
var. *lenticularis*, 169, 172, 183, 218, 220, 221
var. *lipocarpa*, 218, 220, 221, 223
lepidocarpa, 190
leporina, 79
leporinella, 207
leptalea, 128, 149, 150, 153, 155, 157, 158, 159, 259, 266
subsp. *leptalea*, 169, 170, 172, 184
leptonervia, 170, 172, 183
limosa, 107, 148, 149, 150, 153, 154, 158, 159, 160, 169, 171, 172, 183
× *magellanica*, 148
× *rariflora*, 148
×*limula*, 183
livida, 107, 149, 153, 154, 156, 158, 159, 160, 169, 170, 183
lonchocarpa, 112, 127, 128
longebrachiata, 69, 79
longii, 32, 69, 79, 124, 128, 129, 204
louisianica, 33, 79, 128
lucida, 79
lugens, 191
lupuliformis, 130
lupulina, 33, 69, 79, 128
lurida, 128
lutea, 109, 114
maackii, 197, 199, 207, 209
mackenziei, 169, 170, 182, 185
macloviana, 167, 168, 169, 172, 182, 190, 205
macrocephala, 32, 203
macrorrhiza, 79, 202
magellanica, 149, 150, 155, 157, 159, 160, 167, 168
subsp. *irrigua*, 167, 168, 169, 171, 172, 183
subsp. *magellanica*, 167
×*mainensis*, 191
maorica, 79
marina, 163, 169, 171, 174, 182
mariposana, 205
maritima, 167, 168, 169, 170, 177, 182
maximowiczii, 79
meadii, 119, 120–122, 128
media, 163, 174
membranacea, 163, 169, 170, 172, 175, 184
× *utriculata*, 191
×*mendica*, 183
mendocinensis, 190
merritt-fernaldii, 205
michauxiana, 168, 170, 171, 172, 184
microdonta, 107, 128
microglochin, 167, 168, 169, 171, 172, 184, 243, 244, 247–248, 253, 254, 255, 256, 257, 258, 259, 260, 261, 262, 266
subsp. *fuegina*, 167
microptera, 205
miliaris, 191
misera, 188, 190, 192
missouriensis, 205
mitchelliana, 188, 190, 191
molesta, 206
molestiformis, 206
monostachya, 254, 266
montana, 69, 190
morrowii, 27, 70
muehlenbergii, 203
var. *muehlenbergii*, 128
multicostata, 205
muskingumensis, 70, 207
myosurus, 79
nardina, 169, 172, 184, 253, 254, 256, 266
nebrascensis, 32, 70, 80
×*neofilipendula*, 183
nigra, 26, 70, 80, 178, 215, 216, 218, 220, 221, 223–224, 265
subsp. *juncella*, 218
nigricans, 265
nigromarginata, 128
nivalis, 10
normalis, 206
norvegica, 163, 174
subsp. *inferalpina*, 169, 172, 174, 183
subsp. *norvegica*, 169, 172, 174, 183
notha, 80
nubigena, 80
nudata, 70
obtusata, 254, 266
occidentalis, 203
oklahomensis, 26, 32, 70, 80
oligantha, 167
oligosperma, 107, 149, 153, 157, 159, 169, 171, 184
opaca, 32, 206
orbicularis, 53
orizabae, 205
ornithopoda, 70
oronensis, 206
oshimensis, 70
ovalis, 80, 207
oxylepis
var. *oxylepis*, 128
ozarkana, 130, 204
pachystachya, 190, 205
paeninsulae, 110
paleacea, 107, 169, 170, 177, 178, 183
pallescens, 33, 70, 80, 170, 184
panicea, 80
paniculata, 70, 80
pansa, 70
parva, 247, 248, 254, 266
×*patuensis*, 183
pauciflora, 26, 149, 150, 153, 157, 159, 169, 172, 184, 247, 248, 254, 266
paupercula, 167, 168
pellita, 190
pendula, 27, 32, 70

Carex (continued)
pensylvanica, 70, 201, 202
petasata, 207
petricosa
subsp. *misandroides*, 168, 170, 172, 173, 184
petriei, 70
phaeocephala, 207
philocrena, 80
phyllocephala, 70
phyllostachys, 255, 259, 265
physocarpa, 191
×*physocarpoides*, 191
physorhyncha, 124
pilulifera, 70
planata, 198, 201, 203, 210
planispicata, 128
plantaginea, 70
podocarpa, 216, 219, 220, 223
polymorpha, 133–144, 190
polystachya, 266
potosina, 203
praegracilis, 32, 70, 80, 202
prairea, 107, 203
praticola, 169, 170, 172, 182, 207
preslii, 190, 205
projecta, 201, 207
pruinosa, 80
pseudocuraica, 198, 201, 202, 209
pseudocyperus, 70
pulicaris, 255, 266
pumila, 80
pycnostachya, 31, 53, 80
pyrenaica, 254, 266
×*quirponensis*, 183
rariflora, 151, 155, 157, 159, 169, 170, 171, 172, 173, 183, 185, 188, 190
recta, 163, 170, 177, 178, 183
remota, 80, 203, 210, 266
reniformis, 128, 206
retroflexa, 128, 129
rigescens, 33, 80
riparia, 27, 70, 80
rostrata, 33, 80, 149, 151, 153, 154, 157, 158, 159, 163, 169, 172, 175, 184, 191
rotundata, 163, 169, 170, 171, 172, 175, 184, 185, 191
rufina, 172, 183, 215, 218, 220, 221, 223
rupestris, 169, 172, 173, 184, 253, 254, 266
sahnii, 80
salina, 163, 169, 170, 177, 178, 183, 185
sartwellii, 198, 201, 203
saxatilis, 148, 149, 151, 153, 157, 169, 171, 172, 177, 184, 191
saximontana, 191, 227, 228, 233, 234, 235, 236, 237, 239, 240
scaposa, 70
scirpoidea, 187, 189, 193, 255, 256, 261, 266
subsp. *scirpoidea*, 169, 172, 184, 191, 193, 194
scoparia, 206
var. *tessellata*, 206
scopulorum, 215, 220
var. *scopulorum*, 219, 223, 224
secta, 70
senta, 33, 80
shinnersii, 206
siccata, 198, 202, 210
siderosticta, 70
silicea, 204
socialis, 113, 128, 131
solandri, 70
songorica, 53
sororia, 80
specifica, 207
spectabilis, 71
spicata, 80
spissa, 71
squarrosa, 128
stans, 191
×*stenolepsis*, 184, 191
stenoptila, 205
stipata
var. *stipata*, 204
straminea, 206
straminiformis, 206
striatula, 128
stricta, 71, 119, 122, 128, 215, 216, 219, 220, 221, 223, 224
styloflexa, 130
stylosa, 168, 169, 172, 183
subbracteata, 190, 205
suberecta, 206
subfusca, 190, 205
×*subpaleacea*, 183
×*subsalina*, 183
subspathacea, 163, 169, 170, 173, 177, 185
superata, 191, 227, 228, 230, 231, 239
supina
subsp. *spaniocarpa*, 169, 172, 184
sychnocephala, 199, 209, 210–211
sylvatica, 71
tahoensis, 207
temnolepis, 71
tenax, 110, 130
tenera
var. *echinodes*, 206
var. *tenera*, 206
teneriformis, 205
tenuiflora, 151, 155, 156, 169, 171, 172, 182
tereticaulis, 71
testacea, 71, 80
tetrastachya, 206
texensis, 71
thornei, 111
thunbergii, 80, 219, 221, 224
timida, 188, 191, 227, 228, 230, 231, 232, 233, 239
tincta, 206
torta, 219, 223
triangularis, 130
tribuloides, 130, 201
var. *sangamonensis*, 207
var. *tribuloides*, 207
trichocarpa, 107
trifida, 71
trinervis, 219, 224
trisperma, 149, 151, 153, 156, 157, 159, 169, 172, 182
tumulicola, 71
turgescens, 111
typhina, 130
umbellata, 130
umbrosa, 71
uncifolia, 71
unilateralis, 204, 211
ursina, 169, 170, 182
uruguensis, 71, 80
utriculata, 149, 151, 153, 157, 159, 163, 169, 172, 175, 184, 191
vacillans, 178
vaginata, 149, 151, 153, 155, 156, 157, 158, 159, 160, 169, 171, 172, 183
vallis-pulchrae, 253, 265
venusta, 130, 131
vernacula, 201, 202
verrucosa, 33, 80, 112
vesicaria, 149, 169, 172, 184, 191
vestita, 134, 190
vexans, 110, 204
vilmorini, 71
virgata, 71
viridula, 188, 190
subsp. *viridula*, 172
subsp. *viridula* var. *viridula*,

Carex (continued)
169, 184
vulpina, 71, 80
vulpinoidea, 71, 80, 203
willdenowii, 124, 191, 192, 227, 228, 229, 230, 231, 232, 233, 239, 240
var. *megarrhyncha*, 229, 230
williamsii, 169, 171, 172, 174, 183
wootonii, 207
xerantica, 206
Carpha, 24
Castanea
dentata, 142
Castilleja
raupii, 170
Caustis, 3, 54
dioica, 8, 71
Chamaedaphne
calyculata, 147
Cladium, 3, 23, 25, 54, 106, 108
jamaicense, 31, 33–34, 81
mariscoides, 33
mariscus, 81
subsp. *jamaicense*, 12
Cornus, 178
Costularia, 24
Courtoisina, 3, 23, 31, 54
cyperoides, 34, 81
Cymophyllus, 3, 22, 54, 107, 108, 238, 244, 245, 247, 250, 251, 252, 254, 256, 257, 258, 261, 266
fraserianus, 12, 27, 71, 238, 266
Cyperaceae. *see specific genera*
Cyperus, 2, 3, 4, 5, 6, 7, 8, 10, 11, 18, 22–23, 25, 26, 29–30, 31, 32, 34–45, 50, 53, 54, 105, 106, 108, 109, 112, 271
acuminatus, 37, 81
adenophorus, 71
aggregatus, 28, 42, 71, 81
albolutescens, 32
albostriatus, 27, 71, 81
alopecuroides, 24, 39, 71, 81
alternifolius, 3, 4, 6, 9, 12, 38, 54, 81
subsp. *alternifolius*, 38
subsp. *flabelliformis*, 38, 71
alulatus, 81
amabilis, 43, 81
amuricus, 81
arenarius, 42, 81
aristatus, 43
var. *inflexus*, 43
articulatus, 3, 6, 9, 10, 40, 81
babakan, 81
bifax, 35, 81
boreohemisphaericus, 81
bulbosus, 10, 71, 81
capitatus, 8, 71
castaneus, 81
cayennensis, 42
cephalanthus, 111, 113
cephalotes, 24, 82
chordorrhizus, 8, 71
clarus, 72
colymbetes, 24, 25
comans, 27
compactus, 82
compressus, 5, 27, 36, 40, 72, 82
congestus, 72, 82
conglomeratus, 8, 72, 82
var. *effusus*, 5
corymbosus, 3, 6, 8, 82
crassipes, 42, 82
croceus, 41, 72, 82
cuspidatus, 43, 82
cyperinus, 41, 72, 82
cyperoides, 12, 41, 82
subsp. *macrocarpus*, 82
dactylotes, 72
decumbens, 29
dentatus, 42
denudatus, 82
diandrus, 82
diaphanus, 82
difformis, 4, 5, 15, 19, 20, 21, 23, 28, 36, 53, 72, 83
diffusus, 83
digitatus, 40, 83
dilatatus, 83
distans, 4, 41, 83
distinctus, 83, 110, 112
divergens, 44, 45
dives, 24, 83
drummondii, 26
dubius, 83
duclouxii, 83
echinatus, 41, 72, 83
elatus, 24, 83
elegans, 38, 72, 83
engelmannii, 107
entrerianus, 19, 20, 24, 26, 27–29, 30, 37, 72, 83
eragrostis, 20, 27, 37, 38, 72, 84
erythrorhizos, 40, 72, 84
esculentus, 1, 3, 5, 6, 8, 9, 10, 12, 15, 18, 19, 20, 21, 22–24, 26, 35–36, 53, 54, 72, 84
exaltatus, 84
fasciculatus, 44, 84
fertilis, 27, 72
filicinus, 44, 72, 109
flabelliformis, 38
flavescens, 43, 44, 84
flavicomus, 43, 44, 84
flavidus, 43, 84
flavus, 42
floribundus, 41–42, 84
floridanus, 105
foliaceus, 84
fraternus, 37, 113
friburgensis, 84
fugax, 44
fuligineus, 105
fulvus, 84
fuscus, 25, 43, 72, 84
giganteus, 72, 85, 105
glaber, 85
globulosus, 41
glomeratus, 85
gracilinux, 85
gracilis, 43, 72, 85
grandibulbosus, 85
granitophilus, 43
gunnii, 72
hakonensis, 85
haspan, 5, 8, 19, 23, 36–37, 38–39, 72, 85
subsp. *juncoides*, 36
hermaphroditus, 85
houghtonii, 107
hyalinus, 43, 45, 72, 85, 105
hydra, 35
imbricatus, 39, 72, 85
inflexus, 43
intactus, 85
involucratus, 38
iria, 5, 15, 19, 20, 22, 23, 36, 53, 72, 85
isocladus, 39
javanicus, 85
jeminicus, 72
laetus, 85
laevigatus, 45, 72, 85
lanceolatus, 43, 44, 86
latifolius, 86
lecontei, 42, 86, 110
lentiginosus, 105
ligularis, 42, 72, 86
longibracteatus, 86
longus, 27, 72, 86
louisianensis, 44
lucidus, 72
luzulae, 37, 72, 86
macrocephalus, 105
macrostachyos, 86
malaccensis, 86
mapanioides, 86
maranguensis, 86

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Line illustration: *Scirpus microcarpus* (drawing by Tom Reaume). Photos: clockwise from top right: *Carex decomposita*, Bruce Ford; *Carex backii*, Bruce Ford; *Carex annectens*, Robert Naczi; [SEM] *Rhynchospora plumosa*, Robert Naczi; *Carex macrocephala*, Bruce Ford; *Eriophorum angustifolium*, Robert Naczi.

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